Geographical variation in Immaculate Antbird *Myrmeciza immaculata*, with a new subspecies from the Central Andes of Colombia

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SUMMARY.—Morphology, biometrics and vocals indicate that the population of Immaculate Antbird *Myrmeciza immaculata* in Colombia's Central Andes is differentiated from other populations. A new subspecies described here differs from nominate *immaculata* in the underparts coloration of females, reduced feathering on the forehead in adult males and a generally slower song with different note shape. Subspecies rank is assigned because differences between the new taxon and allopatric populations do not attain those between sympatric or parapatric *Myrmeciza*. Available data also support splitting Immaculate Antbird into two species, under any modern version of the Biological Species Concept. Western Immaculate (or Zeledon's) Antbird *M. zeledoni* inhabits foothills and mountains from Costa Rica southwards, and includes *M. z. macrorhyncha* of southern Panama to Ecuador. (Andean) Immaculate Antbird *M. immaculata* occurs in the Central, East, Perijá and Mérida Andes of Colombia and Venezuela (and includes the new subspecies). Vocal differences exceed those between parapatric Goeldi's Antbird *M. goeldii* and White-shouldered Antbird *M. melanoceps* and those between sympatric thamnophilids in other genera. Subspecies *macrorhyncha* and the new subspecies can be considered phylogenetic species within *zeledoni* and *immaculata* respectively. *M. i. affinis* of the Mérida Andes is weakly differentiated from *M. i. immaculata*. None of the features used to diagnose *brunnea* (of the Perijá Mountains) is supported. The name *ellisiana* is a junior synonym of nominate *immaculata*. The name *zeledoni* Ridgway, 1909, is selected to have priority over *berlepschi* Ridgway, 1909 (for which *macrorhyncha* is a replacement name) pursuant to an explicit First Reviser action, to stabilise the name of a split *M. zeledoni*.

Immaculate Antbird *Myrmeciza immaculata* is a large thamnophilid of lower to middle elevations in the mountains and some adjacent lowlands from Central America south to Ecuador and the Andean foothills of Colombia and Venezuela (Zimmer & Isler 2003). Although it has served as a study species for ecologists investigating antbirds at army ant swarms (e.g., Hilty 1974, Willis 1985, Vallely 2001, Rios *et al.* 2008), there has been no detailed study of its taxonomy since Cory & Hellmayr (1924), who lacked vocal data and had only limited specimen material available. Recent years have witnessed various taxonomic revisions of thamnophilids which have often shown historical (largely plumage-based) taxonomy to have under-estimated species richness (e.g., Isler *et al.* 1997, 1998, 1999, 2007, 2008, 2009, Isler & Whitney 2011), including in *Myrmeciza* (Chaves *et al.* 2010).

In *M. immaculata*, it is well known that western and eastern populations differ vocally, with the former having a faster paced song (e.g., Zimmer & Isler 2003, Restall *et al.* 2006, Boesman 2007). Moreover, Salaman *et al.* (2002) considered that a female collected in the Serranía de San Lucas, which lies north of the Central Andes of Colombia, probably represented an undescribed subspecies given morphological differences from other Colombian specimens. However, the convoluted taxonomic history of the group, vague

type localities for some names and lack of sound-recordings from San Lucas complicated describing it. In January 2010, with the improving security situation, TMD participated in a further expedition to the Serranía de San Lucas, obtaining two more specimens and sound-recordings of all four major vocalisations of Immaculate Antbirds there. Together with other recordings from Colombia now available, these materials facilitate an overdue taxonomic study.

In suboscine passerines, vocalisations are considered innate and stereotypical (Kroodsma 1984), and in another suboscine genus, *Scytalopus*, these better reflect molecular differences than plumage characters (Arctander & Fjeldså 1994). Helbig *et al.* (2002) suggested that, to assess the rank of allopatric populations, a comparison of observed differences with those between closely related sympatric or parapatric populations known to be species be undertaken. Based on differences between closely related sympatric species of Thamnophilidae, Isler *et al.* (1998) suggested ranking populations as species given three or more diagnostic vocal differences between them, including at least one in male loudsong. These methods have been widely applied in taxonomic studies of this family (e.g., Isler *et al.* 1999, 2006, 2007, 2009, Chaves *et al.* 2010, Isler & Whitney 2011). Further, sympatric Peruvian Warbling Antbird *Hypocnemis peruviana* and Yellow-breasted Warbling Antbird *H. subflava* show no diagnosable differences in male song, but differ in three characters in their calls (Isler *et al.* 2007). For *Myrmeciza*, in particular, two parapatric or sympatric species (Stub-tailed *M. berlepschi* and Esmeraldas Antbirds *M. nigricauda*) are differentiated by only two subjective differences in male loudsong, although they apparently also differ in calls (Chaves *et al.* 2010) and studies of female songs are needed (Remsen *et al.* 2012). However, these *Myrmeciza* are not closely related to *immaculata* (Brumfield *et al.* 2007) and there are various difficulties with the authors' analysis (Remsen *et al.* 2012). Here, morphology and voice are studied in *Myrmeciza* antbirds considered to be related to *immaculata*.

Methods

Molecular data suggest that *M. immaculata* is sister to Sooty Antbird *M. fortis* among taxa sampled to date, and closely related to White-shouldered Antbird *M. melanoceps* and Goeldi's Antbird *M. goeldii*, based on a sequence of a single specimen of subspecies *zeledoni* from Panama (Brumfield *et al.* 2007). Specimens and sound-recordings of all species in this proposed group were studied to understand better the vocal, biometric and plumage differences between them.

A list of museum acronyms with details of specimens examined and their localities appear in Appendix 1. Details of various Colombian specimens at museums not visited are based on Biomap Alliance Participants (2011). The following measurements were taken for each specimen: wing-chord and tail length (to nearest mm), tarsus length, culmen length from skull to tip of mandible (to nearest 0.5 mm) and, from specimen labels, mass (g), where available. There are a few juveniles in museums, identified by their more patchy or darker rufous plumage. Data from such specimens and, for measurements, from body parts in moult, were excluded from analyses.

Vocalisations of *M. immaculata sensu lato* (Appendix 1), *M. fortis*, *M. goeldii* and *M. melanoceps* were studied. Sonograms were generated using the default settings of Raven Lite 1.0, sometimes adjusted for brightness and then expanded for time period and frequency. *M. immaculata* populations possess several different vocalisations. Four of these, for which reasonable samples were available for most populations, were subject to further study. The loudsong (*sensu* Willis 1967, referred to here as 'song' or 'male song') consists of repeated, relatively melodic, similar notes of generally slower delivery than other vocalisations (Fig. 5). Some recordings feature a second individual calling at a higher acoustic frequency and

often faster with a more irregular note shape and frequency variation, in response to the main singing individual. According to recordists' notes on several recordings, such higher and less regular songs correspond to females duetting. Female and putative female songs were treated separately in the analysis. Two call-types were also found in a significant number of recordings and therefore were subject to further analysis. The first ('single-note call': Fig. 6) consists of a single, sharp note, often repeated usually with significant gaps between calls. The second ('multi-note call') consists of an unmelodic, fast churr varying from a handful of notes to several tens (Fig. 7). Other apparent calls of some taxa include single, isolated notes of similar note shape to those in a song or scold; contact calls including single notes and growls with various note shapes; in-hand distress calls by birds mist-netted; and on one apparent recording of *M. fortis*, a minute-long trill. These other calls were not subject to detailed analysis.

Up to three different examples of each vocalisation type were measured from each single recording analysed, resulting in 1,202 vocalisations being studied, comprising 803 male songs, 108 female songs, 169 multi-note calls and 122 single-note calls. Data on numbers of recordings and sonograms are presented in Appendix 3. Appendix 1 contains a gazetteer of recording localities for *immaculata sensu lato*. Locality data for other recordings are available from the author. Recordings of the same individual were treated as one recording and later recordings were excluded from analyses (and the above data), as were recordings of consecutive or close to consecutive serial number in tapes or recordings made within two hours by the same recordist with similar vocal variables. The number of assumed individuals for each vocalisation for each species is stated in Appendix 3. On most recordings, the first three vocalisations were studied, but in some recordings where the individual approached closer permitting greater definition on the sonograms, later recordings were selected. Songs and multi-note calls were analysed where they comprised a sequence of notes broken by gaps significantly longer than intervals between individual notes in a sequence. Data from recordings that were curtailed or included only fragments of a song or call were ignored. As many recordings from as many localities as possible were included, where available, to determine the full range of variables. All recordings of individuals under natural conditions and after playback were included for the same reason. After compiling the data, the highest and lowest recorded valuables for each variable for each vocalisation for each taxon were double-checked to verify upper and lower limits.

Various vocal variables studied by Isler *et al.* (1999, 2006, 2007, 2009) were considered for further analysis during a preliminary review of sonograms. Data for the following variables were collated and analysed for both male and female songs: (i) number of notes in song; (ii) total song duration; (iii) song speed (calculated by dividing i by ii); (iv) max. acoustic frequency of second note (kHz); (v) max. acoustic frequency of final note (kHz); (vi) acoustic frequency variation (kHz) (iv minus v); (vii) peak in acoustic frequency — the relative position of the highest note (as a percentage, calculated as $(p\text{-}1)/(n\text{-}1)$ where p is the sequential position of the note with the highest frequency and n is the number of notes in the song, and in recordings with no discernible peak or with no ascending or descending pattern, this was instead determined as 'flat' and the recording was ignored); and (viii) position of trough in acoustic frequency — the relative position of the lowest note (expressed as a percentage, see position of peak); (ix) subjective description of individual note shape; and (x) subjective description of change in note shape. The first note of several *M. goeldii* and *M. melanoceps* songs is often doubled or tripled, whilst in other *Myrmeciza* studied here, songs are evenly paced. To provide comparable song speed data with other species, such doubled and tripled notes were treated as a single note for purposes of counting the number

of notes in songs and song speeds. This aspect was instead treated as a feature of note shape and change in note shape for *M. goeldii* and *M. melanoceps*.

For multi-note calls, the same variables were analysed but frequency data were based on the lowest and highest note at any point, rather than particular notes, and the position of peak and trough were based on the time from the start of the call, rather than by counting notes. Multi-note calls often showed harmonic overtones and undertones. The loudest notes for most taxa were typically (though not always) the second highest set of notes (above a single undertone), so this tone was measured for all recordings of the *immaculata* group and *fortis* including in the few recordings where the undertone was louder. For *goeldii* and *melanoceps*, usually only a single tone was visible and in the few recordings with more than one tone overtones were very weak, so the stronger or sole tone was measured.

For single-note calls, only total call duration (= single note length), max. acoustic frequency (kHz) and note shape were studied.

To assess the rank of the new taxon described here, and to consider species and subspecies limits in *M. immaculata*, biometric and vocal data were subdivided on the basis of currently recognised subspecies and well-known biogeographic divides: (i) Venezuelan or Mérida Andes (including the type locality of *affinis*); (ii) East Andes of Colombia (nominate *immaculata*); (iii) Central Andes, Colombia (new subspecies described below); (iv) Chocó lowlands and adjacent foothills from Ecuador north to Darién (*macrorhyncha*); and (v) northern Panama to Costa Rica (*zeledoni*).

Statistical tests.—Various diagnosability tests were made for pairs of vocal and biometric variables of these populations, following Donegan (2008).

LEVEL 1: statistically significant differences at $p<0.05$. A Bonferroni correction was applied for both vocal data and biometrics with the number of variables treated separately for each different call type (male and female songs and multi-note calls: eight variables each, $p<0.0002$; single note calls: two variables, $p<0.025$; biometrics 5 variables $p<0.01$). An unequal variance (Welch's) *t*-test was used; for song speeds, a two-sample Kolmogorov-Smirnov test was applied as an additional test that must be satisfied for Level 1, to account for the possibility of a non-normal distribution. These calculations assess the statistical significance of differences between the means of populations, but do not address diagnosability, as they tolerate considerable overlap.

Further calculations, described below, were undertaken to measure inter-population differences in the context of various species and subspecies concepts. In the formulae used below, $\bar{\chi}_1$ and s_1 are the sample mean and sample standard deviation of Population 1; $\bar{\chi}_2$ and s_2 refer to the same parameters in Population 2; and the *t* value uses a one-sided confidence interval at the percentage specified for the relevant population and variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: a '50% / 97.5%' test, following one of Hubbs & Perlmutter's (1942) subspecies concepts, which is passed if sample means are two average standard deviations or more apart controlling for sample size, i.e. the sample mean of each population falls outside the range of 97.5% of the other population: $|(\bar{\chi}_1 - \bar{\chi}_2)| > (s_1(t_{1 @ 97.5\%}) + s_2(t_{2 @ 97.5\%}))/2$.

LEVEL 3: The traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002), modified to control for sample size, which requires both the following tests to be passed: $|(\bar{\chi}_1 - \bar{\chi}_2)| > s_1(t_{1 @ 99\%}) + s_2(t_{2 @ 75\%})$ and $|(\bar{\chi}_2 - \bar{\chi}_1)| > s_2(t_{2 @ 99\%}) + s_1(t_{1 @ 75\%})$.

LEVEL 4: diagnosability based on recorded values (first part of Isler *et al.*'s 1998 diagnosability test) or, for plumage and subjective vocal characters (note shape and change of note shape), subjective diagnosability.

LEVEL 5: 'Full' diagnosability (where sample means are four average standard deviations apart at the 97.5% level, controlling for sample size) the second part of Isler *et al.*'s (1998) diagnosability test: $|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1\,@\,97.5\%}) + s_2(t_{2\,@\,97.5\%})$.

This analysis resulted in pair-wise differences between eight taxa or groups (49 taxa-pairs) under five different statistical tests for 50 characters, a total of *c*.10,000 pairwise statistical tests. The results of these analyses, together with plumage differences, are set out in Appendix 4.

A separate proposal for ranking species based on scores using a range of characters was recently developed by Tobias *et al.* (2010). Herein, a taxon pair that reaches Level 1 (but does not meet other tests) is treated as conforming to Tobias *et al.*'s (2010) 'minor magnitude' differences (less than two standard deviations between means). Level 2 is equivalent to their 'medium magnitude' (two standard deviations' difference between means), but the statistical test employed is more rigorous in that it also controls for sample size. Tobias *et al.* (2010) use five standard deviations' difference without controlling for sample size for their 'major magnitude' differences; my Level 5 (four standard deviations apart, i.e. no overlap, but controlling for sample size) is treated as equivalent. I do not necessarily endorse any species concept or statistical approach applied in this paper for assessing species rank.

Taxonomic and nomenclatural history

As many as eight different names have been described for *M. immaculata*. Prior to considering species or subspecies limits, it is essential to clarify how described names apply to known populations.

Thamnophilus immaculatus, Lafresnaye, 1845, was based on 'Bogotá' specimens, in a perfunctory description mentioning both male and female plumages. Lafresnaye noted that it was distinguished from other then known antbirds by its uniform, unmarked plumage. Three types (two males and a female-plumaged bird) are now at MCZ (specimen nos. 76756–58; for museum acronyms see Appendix 1). Ten years later, Sclater (1855) described *Pyriglena ellisiana* as a new species, based on a female 'Bogotá' specimen. Sclater (1855) did not mention Lafresnaye's description. Cory & Hellmayr (1924), who later compared the types, considered the female *immaculatus* type and that of *ellisiana* to be identical and that *ellisiana* was therefore a synonym. They also considered the *immaculatus* types to 'agree perfectly' with specimens from near Honda (which, based on elevational data on some specimens in question, were probably collected above this locality, between Honda and Facatativá in the East Andes). Lafresnaye's types are consistent with modern specimens from the East Andes, with the female having rather rufous underparts and the males more feathered lores than in populations further west. The type of *ellisiana* (BMNH 1854.5.5.1) is also typical in plumage of an East Andes specimen. There is white only on the wing bend, which excludes *macrorhyncha*, and the underparts are among the more rufous of East Andes specimens. Although 'Bogotá' collections include birds collected elsewhere in Colombia such as the Central Andes (e.g., Donegan & Avendaño 2010), I concur with Cory & Hellmayr (1924) that both *ellisiana* and *immaculatus* should be treated as referring to the East Andes population, probably collected at mid elevations on the west slope of the East Andes below Bogotá.

Cherrie (1891a,b) described two other taxa as subspecies of *Myrmeciza immaculata*, namely *M. i. occidentalis* (type locality: Pozo Azul, Costa Rica) and *M. i. intermedia* (Talamanca, Costa Rica). However, it is clear that Cherrie did not have a good sample of true *immaculata* to hand. As subsequently noted by Salvin & Godman (1888–97) and confirmed through examination of the types (USNM 11949–50: *occidentalis*; USNM 64715: *intermedia*) both are Chestnut-backed Antbirds *Myrmeciza exsul*. *M. i. occidentalis* is now

generally treated as a subspecies of *M. exsul* whilst *M. i. intermedia* has not been recognised in recent works (e.g., Dickinson 2003, Zimmer & Isler 2003).

The next available name, *M.* [*immaculata*] *berlepschi*, with a type locality of Chimbo, western Ecuador (holotype USNM 97774) was established by Ridgway (1909), who sought to differentiate Chocó populations from nominate *immaculata*. This subspecies is now referred to as *macrorhyncha* Robbins & Ridgely 1993 (see below) and was originally described as a species separate from *immaculata*, diagnosed as having more extensive white markings on the upper wing (in both sexes extending to the lesser coverts) and a larger bill than *immaculata*.

M. zeledoni Ridgway, 1909 (type locality: Guayabo, Costa Rica) was also originally described as a separate species from *berlepschi* and *immaculata*. This name refers to the population in the mountains of northern / western Panama and Costa Rica, and was considered to have biometrics more similar to *berlepschi* than *immaculata*, but with the white wing markings covering only the anterior margin.

Ridgway (1909) noted that nomiate *immaculata* was 'a very different bird' compared to *berlepschi* and *zeledoni* in justifying species rank for all three taxa but Cory & Hellmayr (1924) lumped *zeledoni* and *berlepschi* into *M. immaculata*, recognising all of them as valid subspecies. The same authors also noted differences between Cauca Valley (Central Andes) birds and nominate *immaculata*, considering that 'while typical of *immaculatus* as far as coloration is concerned, [they] approach the western race *berlepschi* by their slightly larger bill and less densely feathered forehead'. Despite this, the Central Andes population apparently lacked further published comment until Salaman *et al.* (2002) reached a similar conclusion to Cory & Hellmayr (1924), considering birds from the northern Central Andes to differ from *berlepschi* and *immaculata*.

Todd (1913) described *M. zeledoni affinis* (type locality: Guarico, Lara, Venezuela) and diagnosed only from *M. zeledoni* of Central America, with no attempt to distinguish it from *berlepschi* or nominate *immaculata*. Cory & Hellmayr (1924) synonymised *affinis* with nominate *immaculata.* They considered the type of *affinis* to be 'practically identical' to the female type of *immaculata* in the 'feathering on the forehead, narrow bill, coloration of the under parts and restriction of white on bend of wing' but also noted that 'additional material from Venezuela should be examined'. Phelps & Phelps (1955) subsequently collected the first specimens from the Perijá in Venezuela and named *M. i. brunnea* based on this series. Robbins & Ridgely (1993) described *M. i. macrorhyncha* as a replacement name for *M. i. berlepschi* due to preoccupation of that name by *Myrmeciza berlepschi* (Hartert, 1898) after Robbins & Ridgely (1991) had transferred *M. berlepschi* to *Myrmeciza* from *Sipia*.

An unidentified antbird was collected in Serranía de los Churumbelos, Cauca, Colombia, in 1998, and was labelled '*Myrmeciza* sp.' in the ICN-UN collection (specimen no. 33244). Salaman *et al.* (1999) reported it as a possible new species. Subsequent review suggests that the specimen represents an undescribed immature male plumage of Spot-winged Antbird *Percnostola leucostigma*, a species common at the locality. It is now labelled as such and databased under that species by Biomap Alliance Participants (2011).

In modern texts, four subspecies of Immaculate Antbird are generally recognised, *immaculata*, *macrorhyncha*, *zeledoni* and *brunnea* (e.g., Hilty & Brown 1986, Ridgely & Tudor 1994, 2009, Salaman *et al.* 2001, 2010, Dickinson 2003, Hilty 2003, Zimmer & Isler 2003, Restall *et al.* 2006). *M. i. immaculata* is treated as occurring in the East and Central Andes of Colombia and the Venezuelan Andes (Hilty & Brown 1986, Hilty 2003, Restall *et al.* 2006). *M. i. brunnea* has been restricted to the Sierra de Perijá (e.g., Hilty & Brown 1986, Hilty 2003) although the name has also been applied to populations on the east slope of the East Andes of Colombia in the Tamá region (Álvarez *et al.* 2007). *M. i. macrorhyncha* occurs in

the western (Chocó) lowlands of Ecuador north to southern Panama as well as on adjacent slopes (Hilty & Brown 1986, Ridgely & Gwynne 1989, Ridgely & Greenfield 2001, Zimmer & Isler 2003), with *M. i. zeledoni* in Costa Rica and northern Panama (Ridgely & Gwynne 1989, Zimmer & Isler 2003). The three other available names—*affinis, berlepschi* and *ellisiana*—are not currently in use for the reasons described above.

Names for the Perijá and Mérida populations

Various data relevant to the taxonomic status of populations in the Mérida Andes (for which the name *affinis* is available), Sierra de Perijá (currently known as *brunnea*) and the nominate population in the East Andes were uncovered during this study. The subjective synonymy of *affinis* with nominate *immaculata* by Cory & Hellmayr (1924) was only tentative and the Táchira depression (which separates the East and Mérida Andes) is an important barrier for subspecies of various premontane birds. Comparison of vocalisations of the East Andes and Mérida Andes populations produced statistically significant mean differences in the acoustic frequency of the second note in male songs, and tentatively, based on small samples, the frequency and length of single-note calls (Appendix 4). Females from the Venezuelan Andes are on average also less strongly rufous on the flanks than specimens from Perijá at COP. However, there may be limited contact between the Mérida and East Andes populations in light of a record close to the depression separating the ranges (Boesman 2007) and distribution mapping, which found the East Andes and Mérida ranges of *immaculata* to be continuous (Fig. 9). *M. i. affinis* could be recognised under more liberal subspecies concepts, but not under those based on full diagnosability or which do not tolerate intermediates. These observed minor variations may be clinal.

The widely recognised subspecies *brunnea* of Perijá is weakly differentiated (if at all) and better treated as a synonym of *immaculata* for now. It was diagnosed from *immaculata* in having 'less rufous, more brownish upper parts' in the female and mandibles being 'greyish white' rather than 'yellowish'. The type of *brunnea* is a female at AMNH (formerly at COP), with a darker brown head and flanks compared to females from the East and Central Andes at AMNH. However, the longer series at COP shows considerable variation in these features and would have been compared directly only with Mérida specimens and one female from the Central Andes in that collection. Photographs of the larger series of females at COP reveals complete overlap in the shade of head, upperparts and underparts between Perijá and Mérida specimens, and this feature is also variable in *immaculata* and the Central Andes population. The only visible difference between Perijá and other specimens at COP is that females have on average slightly more strongly rufous-brown flanks than those in the Central Andes of Colombia and Venezuelan Andes. Differences in bill coloration probably result from comparing old with fresh specimens, as the holotype's bill is now white like other specimens. For example, the Central Andes paratype designated below (collected in 2010) had a greyish mandible when deposited at ICN, whilst the San Lucas paratype (collected in 2001) had the mandible yellowish white by 2010, suggesting decolorisation. The Perijá population appears fully contiguous with *immaculata* further south. Notably, there is a USNM specimen from Ayacucho, Cesar, near the lowest elevation of the 'bridge' between the East Andes and Perijá. Like Perijá specimens, most female *M. i. immaculata* have more strongly rufous flanks than Central Andes specimens. Although no vocal data are available from Perijá and insufficient materials were studied to consider biometric variation, none of the diagnosis of *brunnea* is supported by this study.

Myrmeciza fortis incanescens

Of the other species in this study, only *M. fortis* is historically treated as polytypic. The type locality of *M. fortis* is in Loreto, Peru. Todd (1927) described *M. f. incanescens*, which has been recognised tentatively by most subsequent authors (e.g., Dickinson 2003). However, Zimmer & Isler (2003) considered it of doubtful validity. It was described on the basis of its supposed darker mandible, but incorrectly assumed that the feature was yellow in the nominate. As noted above, original mandible coloration is lost as specimens in this genus age. The type locality of *incanescens* is Tonantins, near the Colombian border of Brazil and the Amazon. Recordings near the *incanescens* type locality (e.g., XC 58407 from Leticia, Colombia, and ML 117193–94 from Amazonas, Brazil) produce vocal data very close to the average for other recordings of *M. fortis*. As a result, the *fortis* sample was not subdivided for analysis. Neither subspecies limits in *M. fortis* nor geographic variation in other *Myrmeciza* species are considered further here.

Genus names

Generic limits in *Myrmeciza* have also been rather fluid. For example, Todd (1927) proposed that *immaculata sensu lato* (including *berlepschi* and *zeledoni*), along with various other species, is better placed in *Myrmelastes* P. L. Sclater, 1858 (of which the type species is Plumbeous Antbird *Myrmeciza hyperythra*). However, Zimmer (1932) considered that the 'genera *Myrmoderus*, *Myrmelastes*, *Myrmophylax*, and *Myrmedestes* are equally unsatisfactory and intergrade insensibly with *Myrmeciza*'. Peters (1951) followed Zimmer (1932) for *Myrmelastes* but adopted some of Todd's (1927) other proposals. Robbins & Ridgely (1991) later sunk *Sipia* into *Myrmeciza*.

Molecular phylogenies suggest that *Myrmeciza* is polyphyletic (Brumfield *et al.* 2007, Tavares *et al.* 2011). The type of the genus, White-bellied Antbird *M. longipes*, was not included in either of these studies, but it would be surprising if it grouped with *immaculata*, *fortis*, *melanoceps* and *goeldii*. If that is the case, another genus name will ultimately be needed for the group studied here. Merging these birds with the apparently related Black-headed Antbird *Percnostola rufifrons*, the *Pyriglena* fire-eyes and / or *Gymnocichla* at generic level may be necessary based on data presented by Brumfield *et al.* (2007). Notably, *ellisiana* was originally described in *Pyriglena* by Sclater (1855) so such a treatment would not be novel. Moreover, *M. goeldii* shares the bright red eye of *Pyriglena* and *Percnostola rufifrons* (others in the clade possess red-brown or rufous to brownish irides) and all of the *Pyriglena* / *Gymnocichla* / *Myrmeciza* clade have fairly uniform black male and brownish female plumages, with some species having white interscapular patches and wing-covert fringes. Songs of *Pyriglena* and *Gymnocichla* are similarly structured to those of *Myrmeciza*, involving repeated notes at more or less the same frequency and with a similar note shape to *zeledoni* and *macrorhyncha* (e.g., Fig. 5). A more rational generic placement of the birds studied here requires further research, so I follow prevailing literature in using *Myrmeciza*.

Description of new subspecies

None of the available names discussed above is associated with a type specimen from the Central Andes. Despite that Cory & Hellmayr (1924) and Salaman *et al.* (2002) drew attention to morphological differences between this and other populations, the Central Andes population is undescribed to date. The following name is proposed:

Myrmeciza immaculata concepcion subsp. nov.

Holotype.—Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN 38162; see also Fig. 1). Adult male collected by TMD above Santa Cecilia, Santa Rosa del Sur municipality, dpto. Bolívar, Colombia, in premontane forest on the east slope of Serranía de San Lucas (07°58'33"N, 74°12'55"W; 1,550 m) on 9 January 2010. Tissue sample (heart) and skeleton also deposited at ICN. The bird foraged with others of the same species and was lured into a mist-net using playback of the song of nominate *M. immaculata* on Álvarez *et al.* (2007). Sound-recordings of the holotype are available on www.xeno-canto. org, see Appendix 1 and Vocalisations.

Paratype.—ICN 38161 is an immature male (with plumage similar to the female) collected by TMD at the type locality on 7 January 2010 (*cf.* Fig. 2).

Other specimens.—ICN 34181 (*cf.* Fig. 3) is an adult female collected by P. G. W. Salaman, A. M. Cuervo & TMD at El Retén, near La Punta, Santa Rosa del Sur, Serranía de San Lucas, Bolívar (08°08'47"N, 74°12'48"W; 1,400 m). (Note: the different coordinates specified in Salaman & Donegan (2001) are widely known to be incorrect. The coordinates here are based on re-geo-referencing of the locality in January 2010.) USNM 392891 is an adult female collected by M. A. Carriker at Volador, Santa Rosa del Sur municipality (*c.*07°58'N, 74°15'W; 800–1,500 m, *per* Paynter 1997), 25 miles west of Simití at 2,600–3,000 ft. USNM 392795 (*cf.* Fig. 4) is an adult male with similar data. Other Central Andes specimens referable to the new subspecies are listed in Appendix 1.

Diagnosis.—Referred to *Myrmeciza* Gray, 1841, due to its medium size for an antbird, resembling *Gymnocichla* but loral and suborbital regions more feathered (only the postocular and rictal regions naked), adult male without white tips to wing-coverts, bill shorter than head and slender to moderately stout, culmen distinctly curved and gonys convex and prominent basally, nostril exposed and lack of rictal bristles, rounded wing, tail rounded, tarsus much longer than culmen and generally uniform, dull plumage (Ridgway 1911), but see Genus names above. Referred to *M. immaculata sensu lato* due to its similar plumage, biometrics and voice to other populations, including its generally uniform black (male) or brown (female) plumages with no strong markings except white on the wing bend and its bluish and whitish bare facial skin. Within *M. immaculata*, it is closest to the nominate subspecies of the adjacent East Andes.

M. i. concepcion has a generally slower song than *M. i. immaculata* which permits >90% of recordings to be identified, although there is marginal overlap (Appendix 3; Figs. 5 & 8). Additionally, in *concepcion* individual notes have shorter termini and most are less downslurred over the first ⅔ of the note than in East and Mérida Andes recordings (Fig. 5). In *concepcion*, single-note calls are given in duets by pairs, with the second (higher) note generally being more downstroke-like or an up-downstroke (Fig. 6) but no other Immaculate Antbird recordings showed duetting in this type of call or similar single-note call shapes.

Morphological differences between the new subspecies and other populations are more subtle. Cory & Hellmayr (1924) considered birds now referred to *concepcion* to have more extensive bare skin and less extensive feathering on the lores and forehead than East Andes specimens. This hypothesis is supported by comparing certain specimens prepared by the same collector (Fig. 4), but it should be regarded as a tentative difference. Female *M. i. concepcion* also has a different (generally less strongly rufous and paler) shade of brown on the flanks and undertail-coverts. Compared to East Andes specimens, *concepcion* is more extensively greyish on the mid-belly (although this is shared by Mérida Andes specimens).

Compared to western *zeledoni* and *macrorhyncha*, male song in the new subspecies differs diagnosably in three or more variables (speed, number of notes and note shape vs. *macrorhyncha*; max. frequency of second note, max. frequency of final note, note shape and change in note shape vs. *zeledoni*) and *concepcion* also differs in its female songs and single-note calls (Appendix 4). The new subspecies also has less extensive white feathering in the upper wing-coverts than these two taxa, the difference from geographically proximate *macrorhyncha* being greatest. *M. i. concepcion* has limited contrast between the shade of brown on the crown (more rufous) and mantle (more brown) whereas in *zeledoni* and *macrorhyncha* these are more concolorous. The female is darker and less rufous overall than *macrorhyncha* (7.5YR 3/4: Fig. 3) and *zeledoni*, with the latter again being more similar to *concepcion* in general plumage shade. Differences between *M. i. concepcion* and *M. fortis*, *M. melanoceps* and *M. goeldii* are set out in Appendix 4.

Description of the holotype.—See Fig. 1. Colours follow Munsell Color (1977, 2000). Description taken immediately after collection. Plumage entirely jet black (uncoded) except white (uncoded) on carpal and wing bend. Iris dark red (10R 3/4), bill black, legs dark grey (Gley 1 3/N), soles cream (2.5YR 8/6). Bare postocular skin very pale blue (uncoded) and in front of eye pastel blue (uncoded). Testes: right 4 mm × 2 mm, left 3.5 mm × 2 mm. Skull 100% ossified. Measurements (mm): wing in life 86.0, tail 84.0, tarsus 33.5, bill 22.0; mass 40.8 g.

Female morphology.—See Fig. 3. The following is based on the San Lucas female at ICN, using the specimen label, with bare-part descriptions and other notes from the label, a photograph and field notes. Crown dark rufous-brown (5YR 2.5/2 but redder). Throat, moustachial and lores sooty grey (10YR 2/1). Upper breast greyish dark brown (7.5YR 3/2), paler on belly, legs and tail-coverts (7.5YR 2.5/3). Rump and mantle dark rufous-brown (5YR 2.5/2 but redder, slightly paler than crown). Tail very dark brown (10YR 2/1). Wings very dark brown (10YR 2/1) with more rufous remiges (5YR 3/3). Legs dark bluish grey with yellowish soles. Bill black, mandible grey on distal two-thirds. Irides dark red. Skull 100% ossified, ovaries 9.0 mm, ovi 2.2 mm. Stomach contents: parts of insects including Coleoptera. Measurements (in mm): wing in life 86.0, wing-chord (skin) 76.5, tail 73.0, tarsus 33.5, bill to skull 22.0 mm; mass 39.3 g.

Variation in the series.—The immature male paratype (Fig. 2) is similar to the female but has the throat, moustachial and lores black (not coded) and upper breast less greyish (7.5YR 2.5/2), iris dark brown (5YR 2.5/2), bill black with basal mandible more greyish (Gley 1 4/N). Bare skin in front of eye bluish (not coded) and behind eye white (not coded). Legs black and soles cream (2.5Y 8/6). Measurements (in mm): wing-chord 79.0, tail 83.0, tarsus 33.5, bill to skull 22.5; mass unknown. Skull 100% ossified. Testes very small (not measured). Stomach contents: ants (Formicidae) and beetles (Chrysomelidae and

Legend to plate on facing page

Figure 1. The male *M. i. concepcion* on which the holotype (ICN 38162) is based, prior to its collection (© B. Huertas)

Figure 2. The immature male *M. i. concepcion* on which the paratype (ICN 38161) is based, prior to its collection (© B. Huertas)

Figure 3. Females of *M. i. concepcion* ICN 34181 (left: female, Serranía San Lucas, Bolívar, Colombia) and *M. z. macrorhynca* ICN 11436 (right: San Antonio de Guaji, Guapi, Cauca, Colombia, collected by A. Olivares, 22 December 1955). Note more extensive white on shoulder of *macrorhyncha* and the differences in plumage shade.

Figure 4. Close-up showing extent of feathering on forehead of males of specimens prepared by M. A. Carriker: (above) *M. i. concepcion* (USNM 392795, Volador, Santa Rosa del Sur, Serranía de San Lucas, Bolívar, 6 May 1947); and (below) *M. i. immaculata* (USNM 411509, Hacienda Santana, Santander, 4 October 1949).
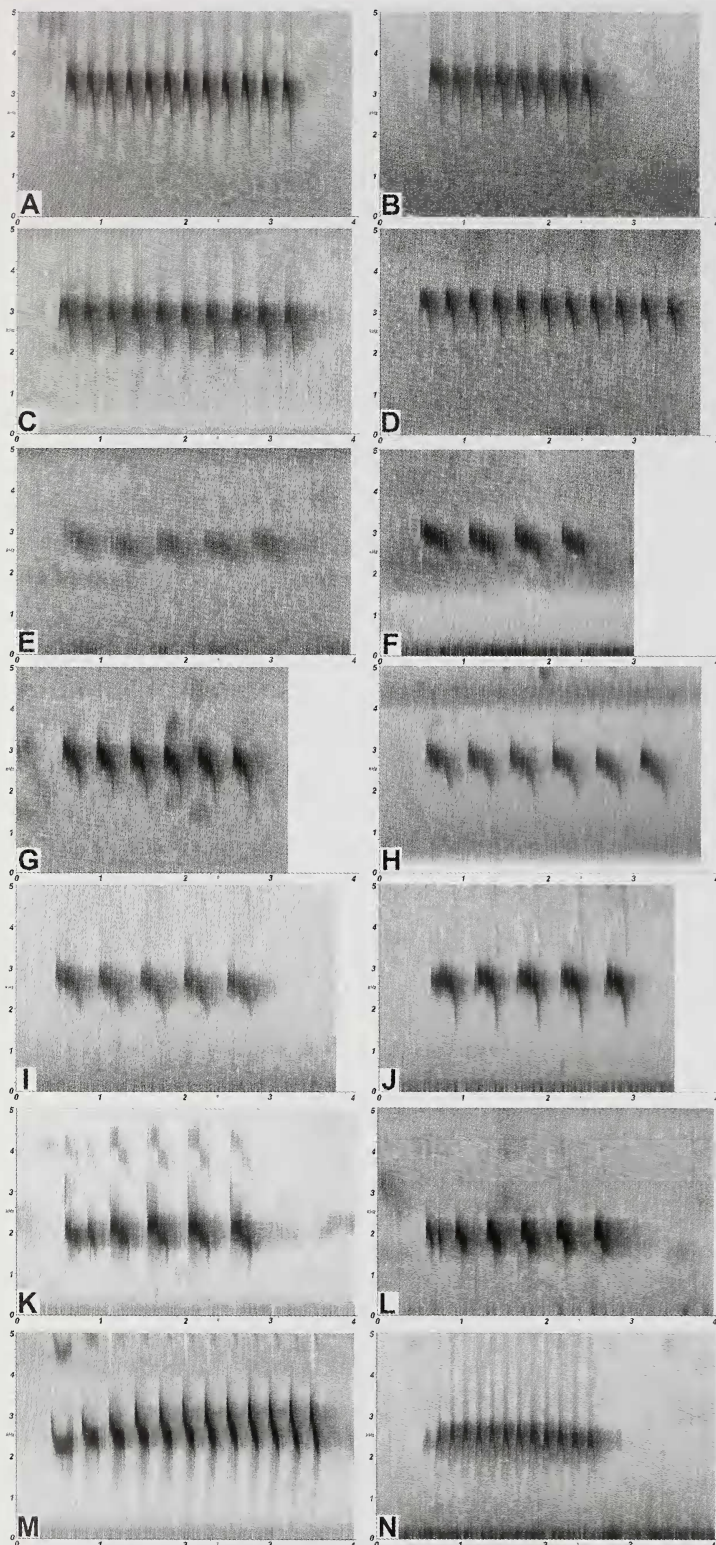
Figure 5. Songs of *Myrmeciza* and other taxa discussed herein. A. *M. z. zeledoni,* Parque Nacional General Omar Torrijos, Coclé, Panama (XC31340: R. Moore). B. *M. z. zeledoni,* La Paz Waterfall Garden, Costa Rica (ISL-KJZ.123:02: K. J. Zimmer). C. *M. z. macrorhyncha,* Tandayapa Bird Lodge, Tandayapa Valley, Pichincha, Ecuador (Moore *et al.* 1999, track 2.13.1: R. S. Ridgely). D. *M. z. macrorhyncha,* Parque Nacional Natural Tatamá, Pueblo Rico, Risaralda, Colombia (XC55196: P. Flórez). E. *M. i. concepcion,* type locality, Colombia, holotype prior to collection (XC92160: T. M. Donegan). F. *M. i. concepcion,* Cañon del río Claro, Antioquia, Colombia (XC18153: H. van Oosten). G. *M. i. immaculata,* Laguna Tabacal, Cundinamarca, Colombia (XC59290: F. Lambert). H. *M. i. immaculata,* Toledo, Parque Nacional Natural Tamá, sector San Isidro, Norte de Santander, Colombia (Álvarez *et al.* 2007, track 4.4(a)). I. *M. i. immaculata,* La Soledad, 20 km north-west of Barinitas, Barinas, Venezuela (XC6086: C. Parrish). J. As previous (XC42299: J. G. Léon). K. *M. melanoceps,* Sucusari Camp, north bank of río Napo, Loreto, Peru (ML34319: T. A. Parker). L. *M. goeldii,* Cocha Cashu Biological Station, Manu National Park, Peru (ML29817: T. A. Parker). M. *M. fortis,* north bank of río Napo, Peru, as above (ML34309: T. A. Parker). N. *Pyriglena leuconota,* El Limo, Loja, Ecuador (XC4240: W. Halfwerk). Note faster song speed and more up-down note shape in A–D (*zeledoni* group) compared to E–J (*immaculata* group) and marginally slower speed and longer 'tails' in *immaculata* (G–J) compared to *concepcion* (E–F). Note also broad similarity in song structure between *Pyriglena leuconota* (N) and *M. zeledoni* (A–D).

Erotylidae). The USNM specimens from San Lucas are an adult male and female, similar to those in the ICN series.

Referring to *macrorhyncha* and *zeledoni*, Willis (1985) suggested that *M. immaculata* has two different plumages before reaching adult male plumage, the first being similar to female plumage and the second like the male but with more brownish-black feathering. This pattern appears to be repeated in *concepcion*, with ICN 38161 an immature male essentially with female plumage; and ICN 18977 and USNM 411507 (from Antioquia) have brownish and black plumage, presumably moutling from immature to adult male plumage. The second phase mentioned by Willis (1985) may only be transient. Two USNM female-plumaged specimens from Valdivia are darker and more rufous than other females of *concepcion* and may be younger birds, but their undertail and flanks still differ in shade from *immaculata*. Data on variation in biometrics and voice of *M. i. concepcion* appear in Appendices 2–3.

Taxonomic rank.—The new taxon is ranked as a subspecies because the vocal differences between it and nominate *immaculata* fall short of Isler *et al.*'s (1998) 'three differences' benchmark for species rank based on voice and morphological differences are slight. Applying the Tobias *et al.* (2010) scoring system, *vis-à-vis* nominate *immaculata*, the new subspecies scores 3 for voice, 2 (tentatively) for bare skin / forehead feathering differences in males and 1 for the different colour of female underparts. Tobias *et al.* (2010) proposed that species should score at least 7 points, leaving *M. i. concepcion* short. Moreover, *M. i. concepcion* responded to playback of *M. i. immaculata* by coming to a mist-net (although it did not sing), also indicating that subspecies rank is appropriate. Recordist notes (XC63733: J. Tobias & N. Sneddon) report that *macrorhyncha* comes to playback of *M. fortis* (but similarly does not vocalise). Whilst such responses may not be fully indicative of conspecificity, a conservative approach is preferred.

Observed vocal differences do not appear to represent clinal variation. The slowest male songs (<1.9 notes / second) are from Tolima (southern Central Andes), Antioquia (northern Central Andes) and Bolívar (Serranía de San Lucas), i.e. across the entire known range of the new subspecies. Moreover, songs of the more proximate East Andes population of *immaculata* average faster than the Mérida population (Appendix 3).

Distribution.—Apparently restricted to the premontane slopes and foothills of the Central Andes, from dpto. Valle del Cauca on the west slope and dpto. Tolima on the east slope, north to Serranía de San Lucas, dpto. Bolívar. The San Lucas range and adjacent northernmost Central Andes near Anorí appear to support an important population, with a slower gradient at suitable elevations compared to further south in the Central Andes.

The southernmost points of the Central and East Andes populations of *M. immaculata* (see Fig. 9) coincide with known major distributional limits of birds in Colombia (Graham *et al.* 2010). The occurrence of related but different taxa in the Central and East Andes is a pattern echoed in several species in the foothill and subtropical zone that occupy the same forests as *M. immaculata*, e.g. Black-winged Saltator *Saltator atripennis*, the woodnymphs *Thalurania fannyi / colombica* and Lineated Foliage-gleaner *Syndactyla subalaris* (e.g., Hilty & Brown 1986).

Notes on the type locality.—The highest elevations of the San Lucas range have long been one of the most exciting remaining examples of terrestrial *tierra incognita*. The mountains reach >2,300 m, are isolated by 100 km below the 1,000 m contour from the nearest mountain range—the Central Andes—and may support other undescribed taxa. Carriker collected here in the 1940s but only reached foothill or lower montane forest, wherein he collected specimens of the new subspecies. In 1998–2002, several attempts were made to study these mountains. Two expeditions were aborted due to the security situation
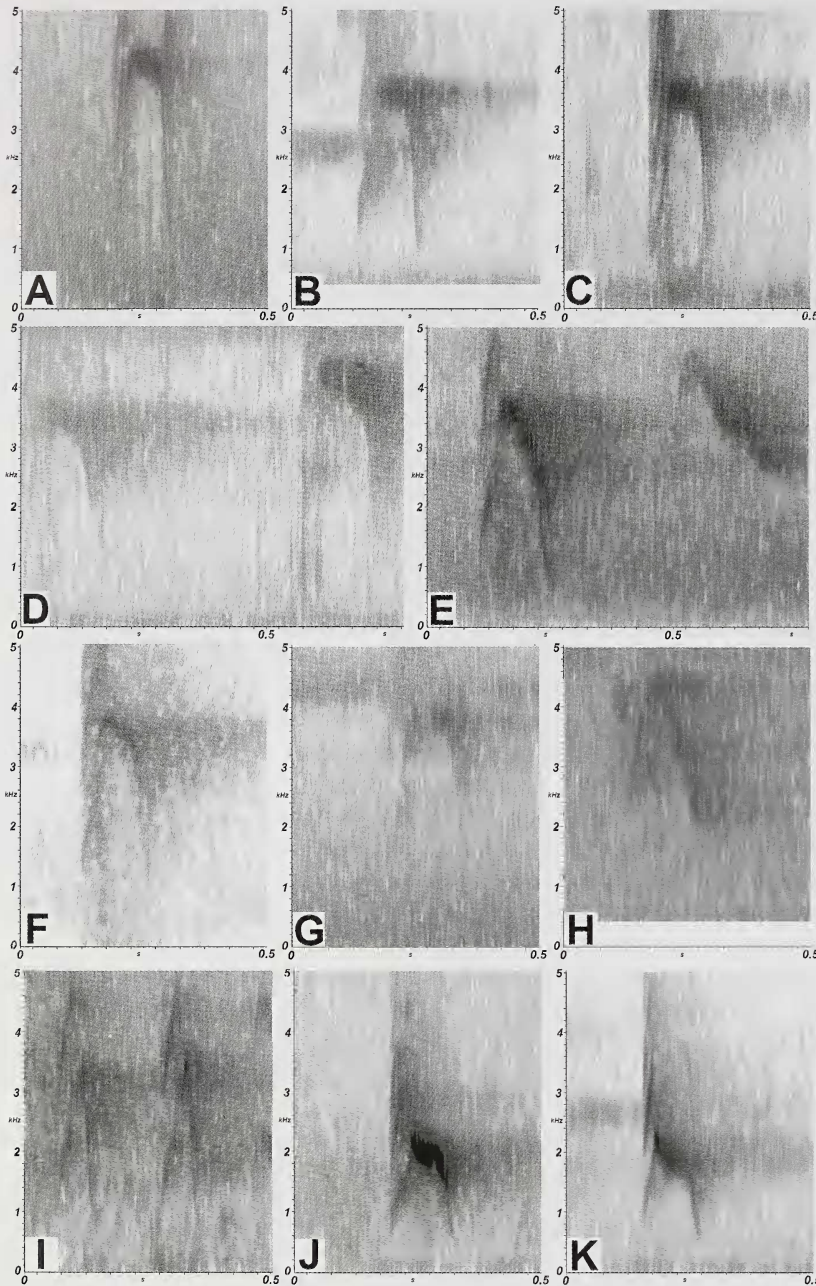
Figure 6. Single-note calls. A. *M. z. zeledoni*, La Virgen del Socorro, Costa Rica (ISL-KJZ.003:24: K. J. Zimmer). B. *M. z. macrorhyncha*, río Anchicayá Valley, Alto Yunda, Valle del Cauca, Colombia (ML83761: S. L. Hilty). C. *M. z. macrorhyncha*, Tinalandia, Pichincha, Ecuador (Krabbe & Nilsson 2003, track 80.15). D. *M. i. concepcion*, duet of group including holotype, type locality (XC92160: T. M. Donegan). E. *M. i. concepcion*, duet, La Pradera, Estación, Risaralda / Antioquia, Colombia (Álvarez *et al*. 2007, track 4.4(c)). F. *M. i. immaculata*, San Isidro, Barinas, Venezuela (XC43139: J. Klaiber). G. *M. i. immaculata*, Toledo, Parque Nacional Natural Tamá, sector San Isidro, Norte de Santander, Colombia (IAVH586: M. Álvarez). H. *M. i. immaculata*, El Talisman, San Vicente de Chucurí, Serranía de los Yariguíes, Santander, Colombia (XC92165: T. M. Donegan). I. *M. fortis*, duet, Huampami, río Cenepa, Amazonas, Peru (ML17544: T. A. Parker). J. *M. melanoceps*, Sabalillo, Loreto, Peru (XC27856: D. Edwards) K. *M. goeldii*, Collpa de Guacamayos, río Tambopata, Madre de Dios (ML75916: C. A. Marantz).

and two others resulted in the participants being detained (Salaman & Donegan 2001). In 2010, with the improving security situation, we managed to get higher than any previous study, with observations to 1,700 m, and studied the interior of premontane forest at the *concepcion* type locality (1,500–1,600 m). However, access to the very highest elevations remains restricted due to security issues and land-use conflicts. Other results of this study will appear elsewhere.

Etymology.—The new subspecies' name is a Spanish-language word *concepcion* and therefore non-variable. The full species and subspecies name taken together are intended to constitute a memorable name, referring to a religious concept recognised by the main branch of Christianity followed in the study region.

Species limits

Novel information relevant to species limits was uncovered during the preparation of the above description. Here, I discuss how various *Myrmeciza* antbirds would be treated under some recently proposed species-ranking tests and concepts.

It has been argued that any re-evaluation of the rank of allopatric populations should first consider observed differences between 'good' sympatric or parapatric species which are closely related (Helbig *et al.* 2002, Remsen 2005). *M. fortis* is sympatric with *M. goeldii* and *M. melanoceps* across broad parts of Amazonia. It exhibits six diagnosable differences in male song from *M. goeldii*, as well as three in female song, three in multi-note calls and two in single-note calls. *M. fortis* also differs considerably in voice from *M. melanoceps*, having four diagnosable differences in male song, two in female song, four in multi-note calls and two in single-note calls (see Appendix 4). In each case, these differences greatly exceed the benchmark for species limits in antbirds suggested by Isler *et al.* (1998).

In contrast, the parapatric and widely recognised species pair *M. goeldii* and *M. melanoceps* showed only two diagnosable differences in male song with none in other calls. These differences are in position of peak (which passed statistical diagnosability tests to Level 5, but limited overlap was observed doubtless due to the very large samples studied) and a subtle difference in note shape change. There were an unusual number of statistically significant but non-diagnosable vocal differences between this taxon pair, with small differences in male loudsongs, female songs and single-note calls, most of which did not reach the Level 2 test of 50% diagnosability. This pair also shows striking differences in extent of bare skin, iris colour and female plumage, such that no recent author has considered lumping them. This species pair presents a further example of minor vocal differentiation between apparently 'good' species of antbirds (*cf.* Isler *et al.* 2007, Chaves *et al.* 2010).

Turning to *M. immaculata*, this group separates into two internally cohesive groups, in both voice and plumage, which meet statistical tests proposed for diagnosing species under the Biological Species Concept. Populations on the west slope of the Andes and adjacent lowlands and in foothill habitats north to Central America differ diagnosably in their songs from the Central, East and Mérida Andes populations based on quantitative data (Appendices 3–4; Fig. 8) and subjectively by note shape (Fig. 5). The two geographically most proximate populations in these groups: *macrorhyncha* (in the West Andes of Colombia) and *concepcion* (Central Andes) differ diagnosably in three variables in adult male songs (number of notes, speed and note shape), two in female songs (number of notes and speed) and in the note shape of single-note calls, i.e. six diagnostic vocal differences. *M. i. concepcion* further differs diagnosably in six vocal variables in male songs from Central American *zeledoni* (number of notes, speed, max. and min. acoustic frequencies, note shape and change in note shape) and in the note shape of single-note calls. A low sample of female
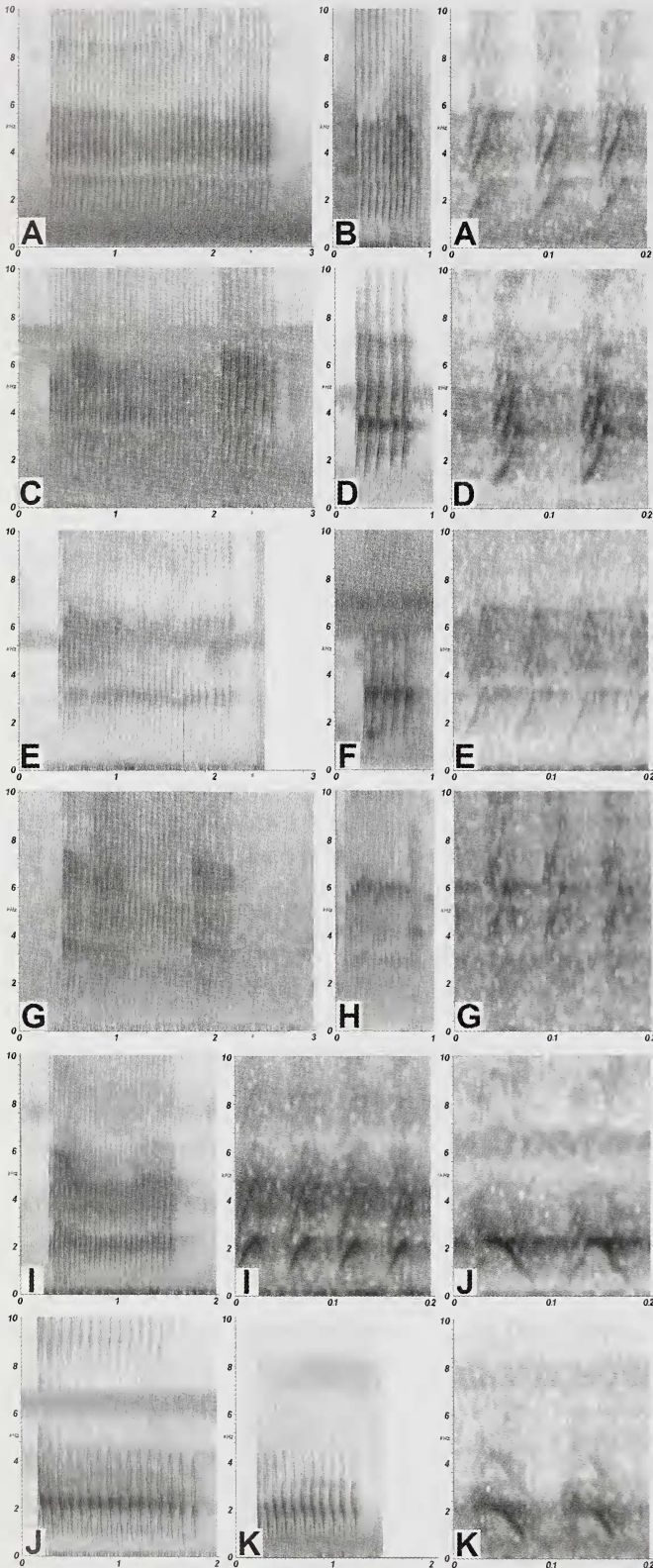
Figure 7. Multi-note calls. For each taxon, sonograms showing examples of entire call and close-up of an extract to show note shape are presented. A. *M. z. zeledoni*, La Virgén del Socorro, Costa Rica (ISL-KJZ.004:17: K. J. Zimmer). B. *M. z. zeledoni*, Boquete road, Bocas del Toro, Panama (ISL-BMW.012:27: B. M. Whitney). C. *M. z. macrorhyncha*, Boca de Cupe, Darién, Panama (ISL-BMW.078:26: B. M. Whitney). D. *M. z. macrorhyncha*, Buenaventura, 9 km west of Piñas, El Oro, Ecuador (Moore *et al.* 1999, track 2.13.4: M. Lysinger). E. *M. i. concepcion*, type locality, Colombia (XC92159: T. M. Donegan). F. *M. i. concepcion*, La Pradera, Estación, Risaralda / Antioquia, Colombia (Álvarez *et al.* 2007, track 4.4(b)). G–H. *M. i. immaculata*, Obra La Toma, Táchira, Venezuela (Boesman 2007). I. *M. fortis*, km 37, Maxus road, south of río Napo, Napo, Ecuador (Krabbe & Nilsson 2003, track 79.10). J. *M. goeldii*, Collpa de Guacamayos, río Tambopata, Madre de Dios, Peru (ML75579: C. A. Marantz). K. *M. melanoceps*, Tiputini Reserve, Ecuador (ISL-KJZ.058:15: K. J. Zimmer).
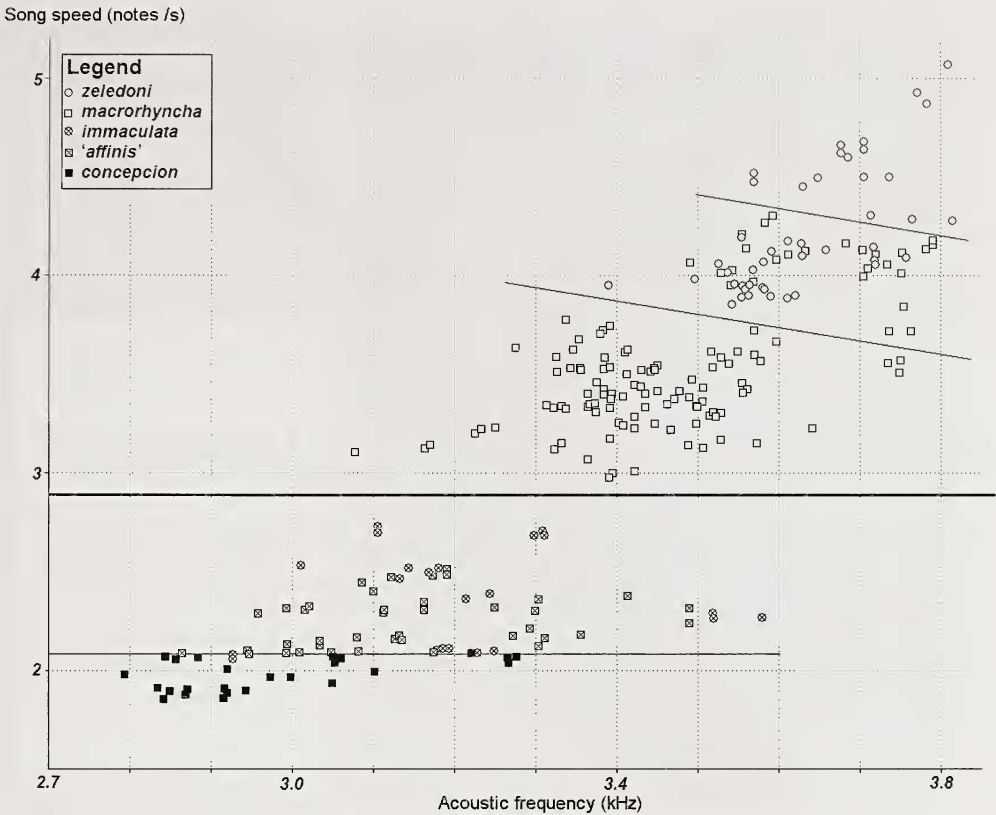
Song speed (notes /s)

Figure 8. Plot of acoustic frequency of second note of song (*x*-axis) vs. song speed (*y*-axis) for all data points for male songs. The complete dark line at song speed = 2.85 notes / second reliably identifies all vocalisations of the two species proposed herein (with all *M. zeledoni* above this line and all *M. immaculata* below it). The narrower, incomplete line at song speed = 2.08 notes / second identifies 94% of *immaculata* recordings (all but 4 of 62) and 93% of *concepcion* recordings (all but 2 of 27). The two narrower, incomplete diagonal lines at higher song speeds show the lower limit of *zeledoni* (lower line) and upper limit of *macrorhyncha* (upper), with the region between them showing the area of overlap in these vocal variables between the taxa.

songs for the Central American population makes diagnosis of relevant variables difficult, but recordings were similar to *macrorhyncha*.

   Pairwise comparisons between nominate *immaculata* and each of *macrorhyncha* and *zeledoni* elucidated only two diagnosable differences in male songs, in speed and note shape (Appendix 4). However, the note shapes of single-note calls of *immaculata* constitute a third diagnostic vocal difference and there are also 2–3 diagnosable differences in female songs. The eastern populations therefore also meet the point of reference for species rank proposed by Isler *et al.* (1998) *vis-à-vis* both *macrorhyncha* and *zeledoni*. Observed differences are consistent with those reported between *M. berlepschi* and *M. nigricauda* (Chaves *et al.* 2010), exceed those between some members of the warbling antbird group ranked as species (Isler *et al.* 2006) and exceed those between *M. goeldii* and *M. melanoceps*.

   Both *zeledoni* and *macrorhyncha* have more extensive white on the upper wing-coverts in both sexes and a different shade of female plumage compared to the eastern taxa. The two groups may also possess different ecological requirements. Subspecies *immaculata* and *concepcion* are restricted to Andean foothill and premontane forests. Records of *M. i.*
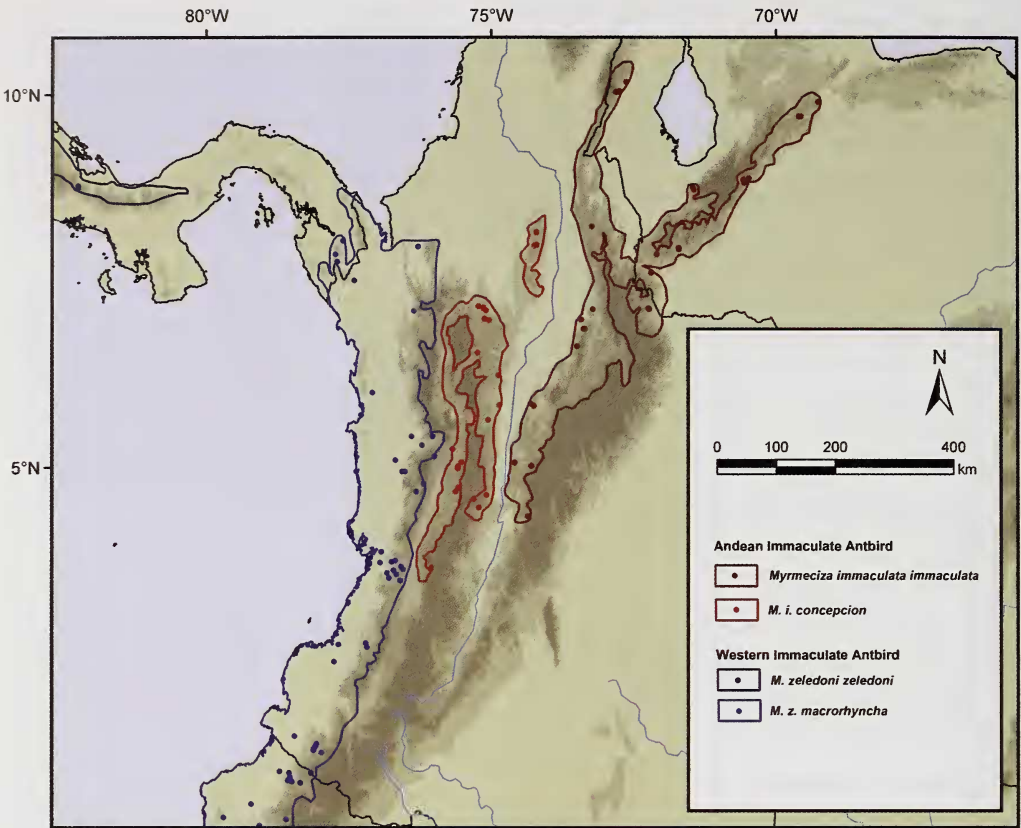
Figure 9. Map showing distribution of *M. immaculata* taxa in Colombia and surrounding regions, based on the new taxonomy established in this paper.

concepcion around Manizales are at 1,300–2,000 m (Verhelst *et al.* 2007), and in San Lucas and Anorí it has been found at 1,400–1,550 m but was not recorded at a nearby site at 800 m (Salaman & Donegan 2001). Similarly, in Serranía de los Yariguíes, *M. i. immaculata* was found at 1,000–2,000 m but not at lower elevations (Donegan *et al.* 2010; *cf.* Appendix 4). All other modern specimens and sound-recordings are from Andean foothill to lower montane regions. The lowest confirmed record of the split *immaculata* group is a sound-recording of *concepcion* at 500 m from the Río Claro reserve, Antioquia. The coordinates of another claimed low-elevation record (Boesman 2007: 500 m) map to a higher elevation. Other low-elevation records, especially in northern Antioquia, pertain to old 'general' collecting localities also found on labels of other higher elevation species of similar age (e.g., Three-striped Warbler *Basileuterus tristriatus*). Although *macrorhyncha* is also found to 2,000 m and *zeledoni* is a foothill and montane bird in Central America, *macrorhyncha* occurs broadly in the Chocó lowlands (at similar latitudes to *immaculata* and *concepcion*) down to sea level (Fig. 9).

Application of Isler *et al.*'s (1998) methodology would result in two separate species being recognised for *immaculata* based on three diagnostic vocal differences. Using the Tobias *et al.* (2010) scoring system, the *immaculata* / *concepcion* vs. *macrorhyncha* / *zeledoni* groups score 1 for biometrics (bill length), 3 for voice (only one character is measured), 3 for the more extensive white shoulder patch in both sexes and conservatively at least 2 (though arguably up to 6) for the different shade of female crown, upperparts and underparts, or a

total of *at least* nine points, exceeding the proposed seven-point test for species rank. It is noteworthy that the Tobias *et al.* (2010) and Isler *et al.* (1998) tests produce similar outcomes, especially given the low weightings in the Tobias *et al.* (2010) tests for vocal characters. Those applying these systems to evaluate species rank should split *M. immaculata* as follows, a return in part to Ridgway's (1909) treatment:

Andean Immaculate Antbird or **Immaculate Antbird** *Myrmeciza immaculata* (Lafresnaye, 1845) includes subspecies *immaculata* Lafresnaye, 1845 (East Andes, Colombia) and *concepcion* (Central Andes, Colombia), along with the doubtful *brunnea* Phelps & Phelps, 1955 (Perijá) and *affinis* Todd, 1917 (Mérida Andes).

Western Immaculate Antbird or **Zeledon's Antbird** *Myrmeciza zeledoni* Ridgway, 1909, including subspecies *zeledoni* Ridgway, 1909 (Costa Rica and northern Panama) and *macrorhyncha* Robbins & Ridgely, 1993 (Ecuador north to southern Panama).

There is a collecting gap between their ranges in the region of Paramillo National Park in the northern foothills of the West Andes (Fig. 9), where subspecies *macrorhyncha* is presumed to occur. The lower slopes have never been extensively collected, nor have they been subject to recent field work due to long-term political instability, and posed a similarly significant gap in connection with the recently proposed split of *M. palliata* (Chaves *et al.* 2010). Although Paramillo should be subject to further study for this and other species if the region stabilises in future, my data suggest that the two groups are sufficiently differentiated in voice that they should be treated as species under the approaches referred to above.

Application of a phylogenetic species concept (e.g., Cracraft 1983) or other diagnosability or pattern-based species concepts would further require *macrohyncha* and *concepcion* to be afforded species rank. The latter two taxa constitute 'groups' within *zeledoni* and *immaculata* respectively, for purposes of checklists that draw attention to such populations (e.g., Schulenberg 2010).

First Reviser action

Taxa *zeledoni* and *berlepschi* were described on the same page by the same author (Ridgway 1909). Neither has priority in the event that they are treated as conspecific (ICZN 1999, Art. 23) because priority between contemporaneously described names can only be determined pursuant to First Reviser action. Their author does not appear to have preferred either name in any subsequent publication. Ridgway (1911) continued to treat them as different species and he died in 1929, after their synonymisation in 1924, without publishing any relevant work in the interim. Because Cory & Hellmayr (1924) subsumed both names into *immaculata*, they did not act as implicit First Reviser either.

Any First Reviser action should stabilise the nomenclature of species that proponents of widely used species concepts are likely to recognise. Notably, the name *berlepschi* would have to be resurrected for *macrorhyncha* if Stub-tailed Antbird *M. berlepschi* were to be placed in a different genus to *M. zeledoni*. *M. berlepschi* is considered related to Chestnut-backed Antbird *M. exsul*, Dull-mantled Antbird *M. laemosticta*, Magdalena Antbird *M. palliata* and *M. nigricauda* (Brumfield *et al.* 2007, Chaves *et al.* 2010). Based on Brumfield *et al.* (2007), various species in *Pyriglena*, *Percnostola*, *Myrmoborus*, *Gymnocichla* and *Percnostola* would have to be lumped when genus limits are revised, if the two *berlepschi* antbirds are to remain congeneric in the long term. Such a far-reaching generic re-arrangement appears

unlikely, especially due to the position of a member of the morphologically distinctive genus, *Myrmoborus*.

The name *zeledoni* Ridgway, 1909, is hereby selected to take priority over *berlepschi* Ridgway, 1909, pursuant to First Reviser action under Art. 24.2 of the Code. Pursuant to ICZN Art. 24A, it is recommended that the name, spelling or nomenclatural act that best serves stability and universality of nomenclature be adopted. Selecting *zeledoni* promotes stability as the species name of western populations would not change due to differing generic arrangements based on this choice. Also, universality considerations could be thought to include 'position precedence' or 'line priority' (under Art. 69A.10, which applies to the fixation of type species for genera) and *zeledoni* appears first in Ridgway (1909).

Vernacular names

Although some commentators prefer new names for components of split species (e.g., Remsen *et al.* 2012), the name 'Immaculate Antbird' remains appropriate even for a split *M. immaculata*, being a direct translation of the species' scientific name. Cory & Hellmayr (1924) used two uninspiring patronyms for the other group: Zeledon's Ant-catcher for *M. i. zeledoni* and Berlepsch's Ant-catcher for *M. i. berlepschi*. No other vernacular names appear ever to have been used. 'Berlepsch's Antbird' would confuse with Stub-tailed Antbird *M. berlepschi* and the name *berlepschi* is currently replaced by *macrorhyncha*. However, Zeledon's Antbird would be available.

Because patronyms convey little information about birds to their main users—birdwatchers—possible alternative names for *M. zeledoni* require consideration. These antbirds do not lend themselves to plumage-based names due to their strong sexual dichromatism. No obvious plumage patterns unite both sexes and the various populations of the new species. Males are uniform black and females uniform brown but Uniform Antshrike (*Thamnophilus unicolor*) could confuse and 'White-shouldered Antbird' is already used for *M. melanoceps*. A good morphological-based name for *zeledoni* is therefore elusive. Similarly, there is no geographic name available to describe the region from western Ecuador to Costa Rica. Arguably the best approach is to use Western Immaculate Antbird (*zeledoni*) and Andean Immaculate Antbird (*immaculata*). They are clearly related and both have been known as Immaculate Antbirds for a long time.

Conservation

Distribution maps produced by BirdLife International (Fig. 9) yield an estimated Extent of Occurrence (EOO) for Andean Immaculate Antbird of $c.92,900$ km^2, comprising $c.64,100$ km^2 for *M. i. immaculata* and $c.28,800$ km^2 for *M. i. concepcion*. The EOO for Western Immaculate Antbird *M. zeledoni* is $c.213,100$ km^2, with $c.18,100$ km^2 for *M. z. zeledoni* and $c.195,000$ km^2 for *M. z. macrorhyncha*. Neither of the split species approaches the max. range size threshold for Vulnerable under criterion B1 of 20,000 km^2 (or Area of Occupancy of 2,000 km^2 for B2), although *zeledoni* and *concepcion* appear to be threatened subspecies. Similarly, range sizes imply that populations of these taxa do not approach as few as 10,000 mature individuals, so criterion C is probably not relevant. It is assumed that only criterion A is potentially relevant for determining threats to these species, with a 30% decline over three generations being the relevant threshold for Vulnerable status. For these antbirds, the relevant time period is estimated at 14 years, based on a generation length of $c.4.8$ years (BirdLife International unpubl. data).

Andean Immaculate Antbird is a forest-dependent species that occurs at low densities. Much of its Andean foothills range is now deforested, coinciding with the main coffee-

growing region of Colombia, and its elevational range in the Central and East Andes is poorly covered by the national parks network. Deforestation in unprotected rural Colombia, such as the Magdalena Valley slopes, has accelerated recently following the return of improved political stability to many regions. Fundación ProAves (2011) recently estimated that other species in the Central and East Andean foothills, e.g., White-mantled Barbet *Capito hypoleucus* and Sooty Ant Tanager *Habia gutturalis*, have incurred habitat losses of 25–30% during the last 10–20 years. These data suggest that Andean Immaculate Antbird could be categorised as Near Threatened on the basis of a population decline approaching 30% over 14 years. There is however some cause for optimism as to the species' future survival: it occurs in various protected areas in Colombia including national parks in Serranía de los Yariguíes and Tamá, and ProAves reserves in Anorí, Antioquia (Arrieto Antioqueño) and Yariguíes (Reinita Cerulea and *Pauxi pauxi* reserves) (Salaman *et al.* 2010). The Río Claro nature reserve in Colombia and Serranía de las Quinchas are also important sites and there are various national parks and other protected areas in the Mérida Andes, where deforestation pressures may be lower.

Western Immaculate Antbird *M. zeledoni* is assumed to be low risk for now. Although the Chocó lowlands are presently subject to unprecedented deforestation threats, the species' broader range includes an array of other habitats and protected areas in Central America particularly, some of which may be subject to reduced rates of habitat conversion. Its population trends should nonetheless be monitored.

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Appendix 1: materials used in analyses

All specimens, sound-recordings and other records used in analyses are cited. For specimens, coordinates are taken from Paynter (1982, 1997), unless otherwise stated. For sound-recordings, coordinates are taken from the relevant database, publication or recordist and converted where necessary. Dashes refer to a series of different specimens or other cat. nos. starting and ending with the number in question. Taxonomy in all appendices follows the new arrangement presented in the main text. Details of specimen and sound-recording materials studied for *M. fortis*, *M. melanoceps* and *M. goeldii* are available on request.

Specimens.—Listed in order of institution and cat. no., with those personally examined listed first, followed by any data from Biomap Alliance Participants (2011). Acronyms: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, Tring (BMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Colección Ornitológica Phelps, Caracas (COP); Cornell University Museum of Vertebrates (CUMV); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH), Museum of Comparative Zoology, Cambridge, MA (MCZ); Museo de Historia Natural, Universidad de la Salle, Bogotá (MLS); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Natural History Museum (LACM); Museum of Natural History, Geneva (MHNG), Smithsonian Institution, National Museum of Natural History, Washington (USNM); Peabody Museum of Natural History, Yale University, Boston (YPM); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Museum of Zoology, University of Michigan (MZUM); Zoologische Staatssammlung, Munich (ZSM); Museo de Historia Natural, Universidad del Cauca, Popayán (MHNUC); Museo de Historia Natural, Universidad del Valle, Cali (MHNUV); and Museum of Vertebrate Zoology, University of California, Berkley (MVZUC).

M. i. immaculata **Mérida, Venezuela**: COP 71720 (Cabudare, Lara, 09°54'N, 69°16'W; 1,200–1,250 m). 81433–34 (Calderas, Barinas, 08°52'N, 70°29'W; 1,250 m) (photographs).

M. i. immaculata **Perijá, Venezuela**: AMNH numbered COP 57616 (holotype) (Barranguilla, Ranchería Julián, Zulia, 10°10'N, 72°38'W; 960 m). COP 57615–23 (Ranchería Julián, as above), 54865–68 (Kunana, Zulia, 10°02'N, 72°47'W; 1,250–1,300 m), 50051 (Ayapa, Zulia, 10°03'N, 72°45'W; 1,100 m), 54864 (Campamento Pejochaina, Zulia, 10°02'N, 72°49'W; 1,700 m), 6441–12 (La Sabana, Zulia, 10°02'N, 72°45'W; 1,400 m) (photographs).

M. i. immaculata **East Andes, Colombia**: AMNH 43321 ('New Grenada'), 121938 (Fusagasugá, Cundinamarca, 04°21'N, 74°22'N; 1,829 m), 121939–40 (Honda, Tolima; 1,829 m, presumably to the east and above this locality). BMNH 1881.2.26.25, 1854.5.5.1 (type of *Pyriglena ellisiana*), 1889.9.20.36, 1889.7.10.75 ('Bogotá'). IAVH 10858 (vereda El Diviso, Toledo, Norte de Santander, 07°07'28"N, 72°14'40"W; 1,100 m). ICN 32830–32 (vereda La Grilla, Serranía de las Quinchas, Otanche, Boyacá, 05°51'N, 74°19'W; 1,300–1,500 m, locality data from Múnera & Laverde 2002). MCZ 76756–58 ('Bogotá': types of *M. immaculata*) (photographs). USNM 373499 (Ayacucho, La Gloria, Cesar, 08°36'N, 73°33'W, locality presumably in East Andes above this) (photograph) (note: allocation to 'East Andes' arbitrary: collecting locality near low pass between Perijá and main East Andes), 373622 (Bellavista, Norte de Santander, 08°13'27"N, 73°14'14"W), 411507–09 (Conchal, Lebrija, Santander, 07°07'N, 73°13'W). Biomap data from **Colombia**: CUMV 7146–48 (El Consuelo, Guaduas, Cundinamarca (above Honda, Tolima; 914 m), 05°04'N, 74°36'W). FMNH 261434 (La Argentina, río Cubugon, Cubará, Boyacá. Paynter's (1997) locality not mapped as too low, presumably near Toledo localities under sound-recordings below). MCZ 47177 ('Bogotá'). MLS 3907 (Fusagasugá). MVZUC 46623 (locality unknown).

M. i. concepcion **Central Andes, Colombia**: AMNH 94924 (Tolima, unknown locality), 108926 (east of Palmira; 2,073 m), Valle del Cauca (c.03°39'N, 76°04'W), 133498–502 (La Frijolera, Antioquia, 07°10'N, 75°25'W, coordinates not used as this and many other species collected here are higher elevation birds), 491460 (Primavera, 07°09'24"N, 75°14'09"W). COP 64620 (La Frijolera) (formerly AMNH 133501,

photograph). IAVH 11969 (Hacienda Tintina, cuenca del río Tapias, Neira, Caldas, 05°14'55"N, 75°41'06"W; 1,080 m). ICN 18977 ('Antioquia'), 34181 (Retén, near La Punta, Serranía de San Lucas, Santa Rosa del Sur, Bolívar, 08°08'47"N, 74°12'48"W; 1,400 m), 38161 (paratype, see above), 38162 (holotype, see above). USNM 392795, 392891 (Volador, Santa Rosa del Sur, Bolívar, 07°58'N, 74°15'W), 436474 (Hacienda La Sofia, Samaná, Caldas, 05°38'N, 75°04'W), 402390–07 (Valdivia, Antioquia, 07°11'N, 75°27'W, coordinates not used as this and many other species collected here are higher elevation birds).

M. zeledoni macrorhyncha: **Panama**: AMNH 135740–03, 135743–48 (Tacarcuna; 731–1,402 m). USNM 238434–38 (Cana, Panama) (photographs). **Colombia**: AMNH 123340 (Bagadó, Chocó, 05°25'N, 76°24'W; 305 m), 123341–42 (Serranía de Baudó, Chocó, 06°00'N, 77°05'W; 914 m) 111935 (Salencio = Nóvita Trail, Alban, Valle del Cauca, 04°47'N, 76°11'W; 1,676 m), 111936 (exchanged to Museu Zoologia, Universidade de São Paulo, Brazil), 111937–41 (Nóvita, Chocó, 04°57'N, 76°34'W; 122 m). BMNH 1910.5.14.[??] (Jimenez, 03°45'N, 76°45'W; *c.*500 m). IAVH 6517 (20 km south-east of Guapí, río Guapí, Cauca, 02°25'24"N, 77°45'21"W). ICN 32275–76 (0.5 km south-east of Altaquer (= Altaguer), Barbacoas, Nariño, 01°15'N, 78°07'W), 31171 (Alto de Pisones, 8 km north-east of Jeguadas, Mistrató, Risaralda, 05°25'N, 76°02'W; 1,400–1,850 m), 5037, 5039 (La Guayacana, Tumaco, Nariño, 01°26'N, 78°27'W), 11435–39 (Guajui, San Antonio, Cauca, 02°39'N, 77°41'W). USNM 428205–06, 443155–58 (río Jurubida, Nuquí, Chocó, 05°50'N, 77°17'W), 443158–60, 443269–71 (Base Baudó, río Nuquí, Chocó, 05°42'N, 77°17'W). **Ecuador**: AMNH 119892–95, 124420–21, 129723–25, 171373, 171375–77, 173291, 173295–97, 180247, 193293, 491461–73 (no details taken). BMNH 1860.11.26.82, 1864.8.9.13 ('Quito'), 1889.9.10.1023 (Intaj), 1889.9.20.34 (Nanegal), 1889.9.20.35 ('Ecuador'), 1925.12.24.514 (Mindo) 1940.12.5.313 (Mindo), 1953.68.640 (Guayabe; 1,000 m), 1953.68.641 (Guayabe, Imbabura). ICN 5038, 5040 (no details taken). USNM 305181 (río de Oro, Manabi), 97774 (Chimbo, holotype of *berlepschi*). **Unknown**: BMNH 1851.9.11.5 ('Brazil'!). Biomap data from **Colombia**: ANSP 157338, 157340, 159567–69, 160020 (La Guayacana, as above), 157995–8001, 158003, 158005–08 (Santa Cecilia, Pueblo Rico, Risaralda, 05°18'N, 76°13'W), 150792–93, 150795–96 (Ricaurte, Nariño, 01°13'N, 77°59'W), 149867–69, 150797 (Perlasvi = río Peasbi, Nariño, 00°57'N, 78°10'W), 146964–65 (río Baudo, Bajo Baudó, Chocó, 04°57'N, 77°22'W), 147198–99 (río Juribida, Nuquí, Chocó, 05°50'N, 77°17'W), 137949, 142388, 144685 (río Mechengue, El Tambo, Cauca, 02°40'N, 77°12'W), 73317 (Córdoba, Buenaventura, Valle del Cauca, 03°53'N, 76°56'W), 73318–21 (Andagoya, Istmina, Chocó, 05°06'N, 76°41'W), 491460 (Primavera, Bolívar, Valle del Cauca, coordinates unknown). CM 66771–73 (Córdoba, Buenaventura, as above), 66121–22, 66174, 66227–28, 66248, 66269, 66287–89, 66347–50, 66390, 66417 (Andagoya, as above), 67685 (La Cumbre, Valle del Cauca, 03°39'N, 76°33'W). FMNH 249731–35, 250839–40 (La Guayacana, as above). LACM 30817, 30848–50, 31273–77 (La Guayacana, as above). MCZ 123414 ('Colombia'), 123415–16 (Palmar, Dagua, Valle del Cauca, 03°35'N, 76°40'W), 123419 (La María, Dagua, Valle del Cauca, 03°38'N, 76°43'W) 123417–18 (Pavas, La Cumbre, Valle del Cauca, 03°41'N, 76°35'W). MHNG 1,168,007 (río Huisitó, El Tambo, Cauca, 02°37'N, 77°11'W), 1,141,004, 1,141,008 (La Guayacana, as above), 1,141,009, 1,142,024 (Ricaurte, as above). MHNUC 1290, 1317 and unnumbered (La Guayacana, as above). MHNUV 3540 (Quebrada Lucas, 2 km from La Desembocadura, río Zabaletas, Buenaventura, Valle del Cauca, 03°44'N, 76°57'W), 5104–05 (río Agua Sucia, Cajambre, Boca, Buenaventura, Valle del Cauca, 03°31'N, 77°19'W), 1054–55, 3126 (Corregimiento Loboguerrero, km 28, Dagua, Valle del Cauca, 03°46'N, 76°41'W; 200–250 m), 1705, 1765 (río Blanco, Pacific slope of West Andes, Valle del Cauca, 03°36'N, 76°50'W), 456, 485 (río Anchicayá, Buenaventura, Valle del Cauca, 03°46'N, 77°10'W; 180–220 m). MZUM 153702–05 (La Guayacana, as above), 222928–29 (Pueblo Rico, as above). LSUMZ 38695–97, 45439 (La Guayacana, as above). YPM 27029, 58729–30 (La Guayacana, as above). ZSM 1910.2373 (Pueblo Rico, as above).

M. z. zeledoni: AMNH 390332–33, 390226 (Costa Rica), 390327–31 (Aquinares, Costa Rica; 1,067 m), 390332–33 (Carrillo, Costa Rica), 390334–35 (Santa Cruz de Turrialba; 1,280 m), 390336 (Bonilla; 610 m), 390337 (La Hondura), 390338 (Navarro; 1,219 m), 491474–77 (Cariblanco de Sarapiqui, Costa Rica); 43320, 43322, 187223–38, 491475 (Panama). BMNH 1889.4.10.70, 1889.9.10.74, 1889.9.10.82, 1889.9.10.93, 1889.9.20.88, 1899.6.1.570–71, 1900.9.30.107–09, 1913.10.15.416, 1949.58.398, 1949.58.399–400, 1969.25.119 (no data taken). USNM 209558 (holotype) (Guayabo, Costa Rica). 476076–77 (Bocas del Toro, río Changuena; 732 m), 95049 (El Naranjo, Costa Rica), 209559 (as holotype).

Sound recordings.—Cat. no. acronyms are as follows: XC = www.xeno-canto.org; IAVH = Instituto Alexander von Humboldt's Colección de Sonidos Ambientales; ML = Macaulay Library, Cornell Lab of Ornithology; AV = AVoCet www.avocet.zoology.msu.edu; IBC = Internet Bird Collection (ibc.lynxeds.com); ISL = Mort & Phyllis Isler's antbird sound library. Localities are listed north to south by taxon and then by country.

M. i. immaculata **Mérida**:
Songs.—**Venezuela** Laguna el Blanquito, PN Yacumbú, Lara (09°42'12"N, 69°34'19"W; 1,450 m) (C. A. Marantz: YAC263 and unnumbered). PN Yacumbú, Lara (09°42'11"N, 69°36'17"W; 1,480 m) (XC6869: N. Athanas; IBC: N. Areta). La Soledad, 20 km north-west of Barinitas, Barinas (08°51'09"N, 70°34'17"W; 1,600–1,630 m) (XC6086: C. Parrish; XC42299: J. G. Leon). San Isidro (08°47'34"N, 70°34'17"W; 1,500 m, XC locality data not used as maps at unfeasibly high elevation, see XC forum 2716) (XC43140–42: J. Klaiber,

first two treated as same recording; ISL-BMW.167:29: B. M. Whitney). Finca Monteverde, Olinda II, Mérida (08°45′N, 71°28′W) (Boesman 2007). Near Azulita, Mérida (08°43′N, 71°27′W; 1,500 m) (ML62071: P. A Schwarz). 13 km east of Santo Domingo, Barinas (ML52704: S. L. Hilty). Obra La Toma, Táchira (07°56′N, 71°43′W; 1,100–1,250 m) (Boesman 2007). 15 km north-east of Táchira, road from San Cristóbal to La Florida, Táchira (07°51′N, 72°06′W; 1,160 m) (ML62072–73: P. A. Schwarz). Unknown locality (ISL-FSM.002:037: R. A. Behrstock). *Female songs.*—**Venezuela** ISL-FSM:002.037 (as above). ML62071 (as above). ML.62072–73 (as above). Obra La Toma, Táchira (Boesman 2007: same recording as above). *Single-note calls.*—**Venezuela** XC7002 (as XC6869). XC43138–40 (as XC43140; latter three treated as same recording). *Multi-note calls.*— **Venezuela** Laguna el Blanquito (as above). Campamento La Trampa, Táchira (07°55′N, 71°43′W; 1,000–1,300 m) (Boesman 2007). Obra La Toma, Táchira (as above but different recording) (Boesman 2007). XC43139 (as above).

M. i. immaculata East Andes:
Male songs.—**Colombia** Toledo, PNN Tamá, sector San Isidro, Norte de Santander (07°07′N, 72°14″W) (IAVH585, IAVH589 (= Álvarez *et al.* 2007, track 4.4(a)): M. Álvarez). Cerro de la Paz, Zapatoca, Santander (06°58′30″N, 73°25′40″W; 1,000 m) (XC24307: T. M. Donegan). Vereda La Ye, Otanche, Boyacá, Serranía de las Quinchas (05°51′N, 74°19′W; 1,450 m: data from Cuervo 2002) (XC12809, 12847–48: O. Laverde). Laguna Tabacal, Cundinamarca (05°01′05″N, 74°18′07″W; 1,350–2,100 m) (XC59290 = AV12579, XC59308: F. Lambert). **Venezuela** río Negro / río Frio area, Táchira (07°36′N, 72°12′W; '400–500 m' (maps to *c*.1,000 m)) (Boesman 2007). *Single-note calls.*—**Colombia** El Taliman, Serranía de los Yariguíes (06°50′57″N, 73°21′51″W; 2,000 m) (XC92165: T. M. Donegan). IAVH586 (as IAVH585).

M. i. concepcion:
Songs.—**Colombia** Type locality (XC92160 (holotype), 92181: T. M. Donegan). La Condena, Antioquia (07°06′N, 75°06′W; 1,600–1,750 m) (IAVH19742: A. M. Cuervo). RNA Arrierito Antioqueño, Anorí, Antioquia (06°59′10″N, 75°07′30″W; 1,450 m) (XC51246: D. Geale; XC55371: P. Flórez). La Pradera (parte alta or Don Matías), Estación, Risaralda or Antioquia (06°32′N, 75°15′W; 1,450 m) (ISL-CDC.001:020: C. D. Cadena; IAVH17831, IAVH19741: A. M. Cuervo). Finca la Estrella, Antioquia (IAVH30217: A. M. Cuervo). Cañon del río Claro, Antioquia (05°50′N, 74°52′W; 600 m) (XC18153: H. van Oosten). Clarita Botero, Ibagué, Tolima (04°28′08″N, 75°13′41″W; 1,450 m) (XC32218: N. Athanas). *Female songs.*—**Colombia** XC55371 (as above). ISL-CDC.001:020 (as above). XC92160 (as above), 92164 (as 92160). *Single-note calls.*—**Colombia** Type locality (XC92160 (group including holotype, as above). IAVH30503–04 (latter = Álvarez *et al.* 2007, track 4.4(c)) (as IAVH17831). *Duet response or downslurred single-note calls.*—**Colombia** Type locality (XC92160, group including holotype, as above). IAVH30484–90 (treated as same recording), IAVH30503–04 (treated as same recording), IAVH30976 (as IAVH17831). *Multi-note calls.*—**Colombia** Type locality (XC92156, 92158–59 (latter two extracts of same recording, details as XC92160 above). Don Matías (as above) (Álvarez *et al.* 2007, track 4.4(b) = ISL-CDC.001:019). *Other calls.*—**Colombia** Type locality (XC92157, 92161–64, as 92160 above) (holotype and other individuals in hand).

M. z. macrorhyncha:
Songs.—**Colombia** PNN Tatamá, Pueblo Rico, Risaralda (05°09′N, 76°00′W; 1,510 m) (XC55196: P. Flórez). Near Buenaventura, Valle (03°53′N, 77°04′W; <100 m) (ISL-SLH.004:06: S. L. Hilty). Río Anchicayá (see specimens, above) (ISL-BBC.001:18: B. B. Coffey). **Ecuador** 18.5 km north-west of Alto Tambo, Esmeraldas (00°58′N, 78°43′W; 450 m) (Krabbe & Nilsson 2003, tracks 80.1–80.2). 20 km north-west of Alto Tambo, Esmeraldas (00°57′N, 78°33′W; 325–400 m) (ML63197: M. B. Robbins). El Placer, Esmeraldas (00°52′N, 78°33′W; 670 m) (ML48920, 48958, 48960, 48975: M. B. Robbins; Krabbe & Nilsson 2003, tracks 80.3–80.4). New camp after INEFAN trail, Esmeraldas (00°51′N, 78°31′W; 925 m) (Krabbe & Nilsson 2003, track 80.9). 0.5 km west of El Placer, Esmeraldas (00°51′N, 78°34′W; 650 m) (ML90003: J. Sterling). Estación Biológica Bilsa (00°22′N, 79°42′W) (XC63733: J. Tobias & N. Seddon). Barcelona, Cordillera Toisán, Imbabura (00°20′N, 78°36′W; 1,850 m) (Krabbe & Nilsson 2003, track 80.12). Reserva Mangaloma, Pichincha (00°07′22″N, 78°59′39″W) (XC76266: I. Davies). 23 km west of Lita, Esmeraldas, (00°06′09″N, 78°33′50″W; 600 m) (XC20970: R. Ahlman). Reserva Maquipucana, Pichincha (00°04′48″N, 78°37′12″W; 1,350–1,600 m) (ML50693: P. Coopmans; XC69122–23: J. P. Kjeldsen). Finca Cuatro Ríos, San Miguel de Los Bancos, Pichincha (00°04′27″N, 78°58′54″W; 800 m) (XC8082: N. Athanas). Milpe, Pichincha (00°01′43″N, 78°51′46″W; 850–1,100 m) (XC8083, 32252: N. Athanas). Tandayapa Bird Lodge, Tandayapa Valley, Pichincha (00°00′36″N, 78°40′39″W; 1,750–1,780 m) (XC3885: N. Athanas; XC54859: M. Nelson; Moore *et al.* 1999, track 2.13.1: R. S. Ridgely). Bellavista, Tandayapa (00°01′S, 78°41′W; 2,300 m) (XC36991: C. Vogt). Septimo Paraíso, Mindo, Pichincha (00°02′37″S, 78°46′35″W; 1,600 m) (XC20006: C. Vogt). Mindo, Pichincha (00°03′08″S, 78°46′35″W; 1,350 m) (XC13020: R. Ahlman). Tinalandia, Pichincha (00°18′S, 79°00′W; 850 m) (Krabbe & Nilsson 2003, track 80.5). Santo Domingo de los Colorados, Tinalandia, south-east of Santo Domingo, Pichincha (00°18′S, 79°08′W) (ML28481, 28591: A. B. van den Berg). Loma Panecillo, Pichincha (00°32′S, 79°07′W; 700 m) (Krabbe & Nilsson 2003, track 80.11). Milpe road (00°08′34″S, 79°08′29″W; 1,067 m) (ML139034: L. R Macaulay). 20 km south of Tinalandia, Santo Domingo, Pichincha (00°20′S, 79°20′W; 700 m) (ML31342: B. Spencer). La Delicia, near La Troncal, Cañar (02°34′S, 79°20′W; 600–900 m) (XC3767: D. Jones). Manta Real, Cañar / Azuay (02°34′S, 79°21′W; 250–1,100 m) (Isler

& Whitney 2002, track 2.97 = ISL-TAP.029:09: T. A. Parker). 8–9 km west of Piñas, El Oro (03°39'S, 79°45'W; 900 m) (Krabbe & Nilsson 2003, tracks 80.6–80.8, 80.10; ISL-BMW.072:12: B. M. Whitney). Buenaventura Reserve, El Oro (03°39'S, 79°46'W; 950–1,000 m) (XC6591: N. Athanas; XC17703: A. Spencer). 4.5 km west of Piñas, El Oro (03°42'S 79°42'W; 900 m) (ML43484: M. B. Robbins). Finca 106.5 (coordinates unknown) (XC63734: J. Tobias & N. Seddon). *Female songs.*—**Colombia** SLH.004:06 (as above). **Ecuador** El Placer, Esmeraldas (00°50'N, 78°30'W; 600–700 m) (track 42.1 Boesman 1999, Boesman 2007). Nanegalito, Pichincha (00°02'N, 75°37'W; 1,525 m) (ML78342: M. B. Robbins). ML28481, 28591, 31342, 90003 (as above). XC63734, 69122 (as above). Tracks 80.1–80.3 in Krabbe & Nilsson 2003 (as above). *Single-note calls.*—**Panama** Cana, Darién (07°45'N, 77°42'W; 550–650 m) (ISL-BMW.011:28: B. M. Whitney). ML25767 (as below). **Colombia** Anchicayá Valley at Alto Yunda, Valle del Cauca (03°32'N, 76°48'W; 1,000 m) (ML83761: S. L. Hilty). **Ecuador** Tinalandia, Pichincha (00°16'48"S, 79°04'48"W) (ML84416: R. A. Rowlett). Tinalandia (as others in Krabbe & Nilsson 2003, track 80.15). 20 km north-east of Pedro Vicente, Maldonado, Pichincha (00°15'00"N, 79°04'11"W; 500 m) (XC71228, 71230, 71232–33 (all treated as same individual = ISL-DFL.004:11): D. F. Lane). 17 km north-west of Pedro Vicente, Maldonado, Pichincha (00°08'09"N, 79°08'02"W; 370 m) (XC71261 (= ISL-DFL.004:06): D. F. Lane). Silanche, Pichincha (00°06'N, 79°04'W; 450–500 m) (Krabbe & Nilsson 2003, track 80.16). Maquipucuna, Pichincha (00°05'N, 78°37'W; 1,850–1,950 m) (Krabbe & Nilsson 2003, track 80.17). North-east of Salanguilla, Guayas (01°48'S, 80°32'W; 620 m) (Krabbe & Nilsson 2003, tracks 80.14, 80.18). Buenaventura, 9 km west of Piñas, El Oro (03°39'S, 79°45'W; 900–1,000 m) (Moore *et al.* 1999, track 2.13.3: P. Coopmans). Barcelona, Cordillera Toisán (as above) (Krabbe & Nilsson 2003, track 80.21). 18.5 km north-west of Alto Tambo (as above) (Krabbe & Nilsson 2003, track 80.13). ISL-TAP.029:09 (as above). ML48958 (as above), ML50694 (as ML50693), ML80961 (as ML50693 but G. F. Budney), ML139034 (as above), XC6626 (as XC3885), XC54860 (as XC54859). *Multi-note calls.*—**Panama** Boca de Cupe, Darién (08°02'N, 77°36'W; 500 m) (ISL-BMW.078:26: B. M. Whitney). Cerro Pirre, Darién, (07°51'N, 77°44'W; 500–800 m) (ISL-BMW.002:09, 011:13, 011:30: B. M. Whitney). Cana, Darién (07°50'N, 77°40'W; 600–1,700 m) (Boesman 1999, track 42.2 = Boesman 2007; ML25767: T. A. Parker; ML105191: L. R Macaulay). ISL-BMW.011:28 (as above). **Colombia** Alto Anchiyaya, Valle del Cauca (03°30'N, 76°36'W; 600 m) (XC68783 = AV9207: F. Lambert). Altaquer, RN Río Ñambí, Nariño (01°18'N, 78°05'W; 1,100–1,600 m) (XC12846: O. Laverde). **Ecuador** 2.7 km east of Alto Tambo, Esmeraldas (00°53'31"N, 78°31'58"W; 890 m) (XC72663: D. F. Lane (= ISL-DFL.005:06)). Milpe road, Mindo (00°06'56"S, 78°25'03"W; 1,185 m) (ML139004: L. R. Macaulay). Near Piñas, El Oro (03°40'S, 79°39'W; 1,200 m) (XC9836: A. T. Chartier). Maquipucuna (as above) (Krabbe & Nilsson 2003, track 80.19). Buenaventura (as above) (Moore *et al.* 1999, track 2.13.4: M. Lysinger). El Placer (as above) (Krabbe & Nilsson 2003, track 80.20). Mindo (as above) (Moore *et al.* 1999, track 2.13.2). Krabbe & Nilsson (2003, tracks 80.17, 80.18) (as above). ISL-BMW.035:02 (as ISL-BMW.072:12). ML50689 (as ML50693), ML50694 (as above), XC3766 (as XC3767), XC54860 (as above), XC71261 (as above). *Other call.*—**Ecuador** río Bogotá, Alto Tambo, Esmeraldas (00°07'N, 78°41'W; 700 m) (XC13022: R. Ahlman: see XC forum 1831).

M. z. zeledoni:
Songs.—**Costa Rica** PN Braulio Carillo, San José (10°10'N, 83°58'W) (ISL-KJZ.018:22: K. J. Zimmer). Monteverde Cloud Forest Reserve (10°18'36"N, 84°48'25"W) (XC62677: J. King). Monteverde, Peñas Blancas, Alajuela (10°18'N, 83°48'W; 800 m) (ML72871: D. L. Ross; Ross & Whitney 1995, track 94 (= Ross 1998, track 56; = one of ML72878, 72880 or 72896); ISL-BMW.009:05: B. M. Whitney). La Virgen del Socorro (ISL-KJZ.004:17–18, ISL-KJZ.003:24 (=ISL-KJZ.003:10) & ISL-KJZ.123:29 (=ISL-KJZ135:29): K. J. Zimmer). Unknown locality (ISL-KJZ.095:01, 095:18: K. J. Zimmer). La Paz Waterfall Garden (ISL-KJZ.123:02 (=ISL-KJZ.135:02): K. J. Zimmer). Puntarenas (1,650 m) (ML53917: D. L. Ross). Finca Fernández, Chiriquí (ISL-BMW.011:03: B. M. Whitney). **Panama** Gualaca–Chiriquí road, Chiriquí (08°46'N, 82°15'W; 1,175 m) (ML54407: M. B. Robbins). PN General Omar Torrijos, Coclé (700 m) (XC31340: R. Moore). Finca Fernandez, Chiriqui (ISL-BMW.011:03: B. M. Whitney). *Female songs.*—**Costa Rica** ISL-KJZ.004:18 (as above). **Panama** ML54407 (as above). *Single-note calls.*—**Costa Rica** ISL-KJZ.003:24 (as above). **Panama** Boquete road, upper Caribbean slope, Bocas del Toro (>800 m) (ISL-BMW.012:27). *Multi-note calls.*—**Costa Rica** ISL-KJZ.004:17–18 (as above). ISL-BMW.012:27 (as above).

Other locality data.—These comprise data from the literature, as well as ML sound-recordings from localities not mentioned above and not presently available in digital form or Isler database recordings not requested from different localities to those above. IAVH = Instituto Alexander von Humboldt AICAs database (http://aicas.humboldt.org.co).

M. i. immaculata **Mérida Andes, Venezuela** Lower Santo Domingo Valley (08°48'32"N, 70°33'43"W; P. Boesman *in litt.* 2011) (Boesman 1998). **East Andes, Colombia** Cerro de la Paz, Zapatoca, Santander, east and west slopes, (06°59'N, 73°26'W; 1,000–1,300 m) (Donegan *et al.* 2010). RNA Reinita Cerulea (06°51'N, 73°23'W; 1,700 m) (Salaman *et al.* 2010). Alto Honduras, El Carmen, Serranía de los Yariguíes, Santander (06°37'N, 73°30'W; 1,600 m) (Donegan *et al.* 2010). Note record in Donegan *et al.* (2010) at Bajo Simacota, Santander (06°46'N, 73°44'W; 100–150 m) was based on a recording of Bare-crowned Antbird *Gymnocichla nudiceps*.

M. i. concepcion **Colombia** Santa Gertrudis (07°08'N, 75°09'W; 1,420–1,470 m); Bodega Vieja, Antioquia (06°58'N, 75°03'W; 1,300–1,550 m) (Cuervo *et al.* 2008). Embalse de Punchiná, Antioquia (06°14'N, 74°53'W;

200–800 m) (IAVH). Ecoparque Los Alcázares, Manizales, Caldas (05°04′06″N, 75°31′58″W) (Verhelst *et al.* 2007). Playarica, Manizales, Caldas (05°00′54″N, 75°35′20″W) (Verhelst *et al.* 2007). Estación Cenicafé, Manizales, Caldas (04°59′28″N, 75°35′30″W; 1,310–1,425 m) (Verhelst *et al.* 2007, coordinates for last three localities from J. C. Verhelest *in litt.* 2011). Santuario de Flora y Fauna Otún Quimbaya (04°44′01″N, 75°35′16″W; 1,800–2,100 m) (Rios *et al.* 2008). Cañón del río Barbas y Bremen, Risaralda (04°41′N, 75°38′W; 1,600–2,100 m) (IAVH). La Cascada, Tolima (04°35′N, 75°19′W) (A. Quevedo *in litt.* 2011 / ProAves photograph). Anzoategui, Tolima (04°38′27″N, 75°05′03″W) (A. Quevedo *in litt.* 2011).

M. zeledoni macrorhyncha **Panama** 10 km north of Los Planes, Fortuna Field Station, Chiriquí (08°44′N, 82°15′W; 1,000 m) (ML144050: M. B. Robbins). Gualea (00°07′N, 78°44′W) (Willis 1985), Paramba (00°49′N 78°21′W) (Willis 1985). **Colombia** Tucurá, Córdoba (07°57′N, 76°17′W) (Willis 1985). Serranía de Abibe, Chocó (07°05′17″N, 76°21′37″W; 1,500 m) (C. Olaciregui *in litt.* 2011). El Tigre, Chocó (04°57′N, 76°31′W) (Willis 1985). Serranía de los Paraguas, Chocó (04°41′N, 76°19′W; 300–2,700 m) (IAVH). Anchicayá Valley (03°32′N, 76°48′W; 980–1,250 m) (Hilty 1974). RN El Pangán, Nariño (01°20′N, 78°04′W; 600–1,990 m) (Salaman *et al.* 2010; IAVH). RN Río Nambí, Nariño (01°16′N, 78°07′W; 1,100–1,600 m) (IAVH). **Ecuador** Canandé, Esmeraldas (00°32′N, 79°13′W; 570 m) (ISL-NK_C_136: N. Krabbe). Faisón, Estación, Pichincha (00°20′S, 78°52′W) (ISL-RAB.009.19: R. A. Behrstock). Río Palenque, Los Ríos (00°33′S, 79°22′W; 200–300 m) (ISL-BBC.005:21, 25–26: B. B. Coffey). Above Manta Real, Cañar, Ecuador (02°34′S, 79°21′W) (ML80799: T. A. Parker).

Appendix 2: biometrics

Data are presented as follows: mean ± standard deviation (lowest value–highest value) (n = no. of specimens or individuals).

Taxon	Wing-chord from skins (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)	Body mass (g)
M. i. brunnea (female holotype)	74.0 (n=1)	73.0 (n=1)	32.0 (n=1)	21.0 (n=1)	/
M. i. immaculata (all East Andes)	80.16 ± 3.33 (76.5–89.0) (n=15)	76.52 ± 3.82 (70–83) (n=15)	32.96 ± 1.05 (31.4–34.7) (n=16)	21.24 ± 1.04 (19.5–22.5) (n=16)	41.3 ± 2.46 (38.7–43.6) (n=3)
Males	79.87 ± 3.36 (76.5–89.0) (n=11)	76.24 ± 3.96 (70–83) (n=11)	33.02 ± 1.18 (31.4–34.7) (n=12)	21.28 ± 1.05 (19.5–22.5) (n=12)	42.6 ± 1.41 (41.6–43.6) (n=2)
Females	80.95 ± 3.62 (78–86) (n=4)	77.28 ± 3.86 (72–81) (n=4)	32.78 ± 0.66 (32.0–33.5) (n=4)	21.10 ± 1.14 (19.9–22.5) (n=4)	38.7 (n=1)
M. i. concepcion Specimens	79.07 ± 2.68 (74–86) (n=20)	74.76 ± 3.84 (69–84) (n=20)	33.36 ± 0.84 (31.8–35.5) (n=20)	21.90 ± 0.78 (20.7–23.5) (n=18)	40.05 ± 1.06 (39.3–40.8) (n=2)
Males	80.08 ± 2.85 (74–86) (n=12)	76.34 ± 4.05 (72–84) (n=12)	33.42 ± 1.07 (31.8–35.5) (n=12)	21.99 ± 0.97 (20.7–23.5) (n=10)	40.8 (n=1)
Females	77.55 ± 1.52 (75–80) (n=8)	72.39 ± 1.87 (69–75) (n=8)	33.26 ± 0.36 (32.6–33.5) (n=8)	21.78 ± 0.52 (21.0–22.5) (n=8)	39.3 (n=1)
M. i. concepcion Live birds	83.00 ± 3.10 (79–86) (n=6)	82.40 ± 3.53 (67–85) (n=4)	33.27 ± 0.76 (32.1–34.0) (n=6)	21.47 ± 0.84 (20.5–22.5) (n=6)	40.67 ± 1.01 (39.3–41.6) (n=5)
Males	83.60 ± 3.05 (79–86) (n=5)	84.10 ± 1.15 (83–85.3) (n=3)	33.14 ± 0.77 (32.1–34.0) (n=5)	21.66 ± 0.77 (20.7–22.5) (n=5)	41.00 ± 0.77 (40.0–41.6) (n=4)
Females	80.0 (n=1)	77.3 (n=1)	33.9 (n=1)	20.50 (n=1)	39.30 (n=1)
M. z. macrorhyncha	80.55 ± 3.32 (73–88) (n=117)	70.91 ± 3.52 (63–84) (n=113)	35.49 ± 1.46 (31.6–38.5) (n=115)	23.11 ± 1.08 (20.0–25.5) (n=113)	44.9 ± 4.42 (39.9–48.3) (n=3)
Males	81.53 ± 3.36 (74–88) (n=65)	72.12 ± 3.56 (63–84) (n=64)	35.68 ± 1.37 (32.5–38.5) (n=65)	23.40 ± 0.94 (21.5–25.5) (n=64)	44.1 ± 5.94 (39.9–48.3) (n=2)
Females	79.32 ± 2.84 (73–88) (n=52)	69.33 ± 2.78 (63–76) (n=49)	35.25 ± 1.54 (31.6–38.5) (n=50)	22.73 ± 1.15 (20–25) (n=49)	46.5 (n=1)
M. z. zeledoni	78.18 ± 3.11 (72–85) (n=54)	72.85 ± 3.62 (61–82) (n=53)	33.93 ± 1.16 (30.3–36.0) (n=54)	22.72 ± 0.84 (20.0–24.5) (n=52)	/
Males	78.86 ± 2.82 (72–85) (n=32)	73.21 ± 3.99 (61–82) (n=31)	34.07 ± 1.16 (30.3–36.0) (n=32)	22.89 ± 0.69 (22.0–24.5) (n=30)	/
Females	77.20 ± 3.31 (73–85) (n=22)	72.35 ± 3.05 (67–78) (n=22)	33.71 ± 1.15 (32.0–35.7) (n=22)	22.48 ± 0.97 (20–24) (n=22)	/
M. fortis	81.90 ± 1.84 (78–86) (n=39)	64.27 ± 3.32 (54–71) (n=39)	34.44 ± 1.03 (32–37) (n=39)	22.70 ± 1.04 (20–26) (n=38)	/

Males	82.04 ± 1.53 (78–85) (n=26)	65.08 ± 3.55 (54–71) (n=26)	34.69 ± 0.98 (32.5–37.0) (n=26)	22.69 ± 1.14 (20–26) (n=26)	/
Females	81.62 ± 2.40 (78–86) (n=13)	62.65 ± 2.09 (58–67) (n=13)	33.92 ± 0.95 (32.0–35.5) (n=13)	22.71 ± 0.84 (21–24) (n=12)	/
Live data (Churumbelos, Cauca, Colombia)	83.00 (n=1)	/	/	/	54.00 (n=1)
M. melanoceps	84.23 ± 2.85 (78–91) (n=28)	58.31 ± 3.38 (52–64) (n=26)	32.15 ± 1.16 (30.0–34.5) (n=16)	24.04 ± 1.00 (21.0–25.5) (n=28)	/
Males	86.00 ± 2.48 (80–91) (n=15)	60.36 ± 2.10 (57–64) (n=14)	32.23 ± 1.33 (30.0–34.5) (n=13)	24.4 ± 0.82 (22.5–25.5) (n=13)	/
Females	82.19 ± 1.65 (78–85) (n=13)	55.92 ± 3.03 (52–60) (n=12)	32.08 ± 1.00 (31–34) (n=13)	23.62 ± 1.04 (21–25) (n=13)	/
M. goeldii	85.67 ± 3.51 (82–89) (n=3)	65.00 ± 2.65 (63–68) (n=3)	35.17 ± 1.26 (34.0–36.5) (n=3)	24.00 ± 1.32 (23.0–25.5) (n=3)	/
Males	87.50 ± 2.12 (86–89) (n=2)	65.50 ± 3.54 (63–68) (n=2)	35.75 ± 1.06 (35.0–36.5) (n=2)	24.50 ± 1.41 (23.5–25.5) (n=2)	/
Females	82.0 (n=1)	64.0 (n=1)	34.0 (n=1)	23.0 (n=1)	/

Appendix 3: vocal data

In each table in this appendix, for each taxon / song, data are presented as follows: mean ± standard deviation (lowest value–highest value) (n = no. of vocalisations analysed). n_{ai}=x in respect of each vocalisation for each population, refers to the assumed no. of individuals sampled.

A. Male songs

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of second note (kHz)	Max. frequency of last note (kHz)	Frequency variation (kHz)	Position of peak (%)	Position of trough (%)
M. i. immaculata Mérida Andes, Venezuela (n_{ai}=16)	5.33 ± 0.98 (3–7) (n=39)	2.39 ± 0.45 (1.25–3.37) (n=39)	2.24 ± 0.14 (2.06–2.51) (n=39)	3.11 ± 0.13 (2.86–3.36) (n=39)	3.06 ± 0.13 (2.86–3.32) (n=38)	0.05 ± 0.05 (-0.02–0.14) (n=38)	0.00 ± 0.01 (0.00–0.08) (n=32)	0.95 ± 0.07 (0.75–1.00) (n=30)
M. i. immaculata East Andes, Colombia (n_{ai}=9)	5.65 ± 0.94 (4–8) (n=23)	2.38 ± 0.45 (1.47–3.21) (n=23)	2.40 ± 0.22 (2.09–2.72) (n=23)	3.27 ± 0.16 (3.01–3.58) (n=23)	3.17 ± 0.14 (3.00–3.43) (n=23)	0.10 ± 0.05 (0.01–0.20) (n=23)	0.04 ± 0.09 (0.00–0.25) (n=22)	0.98 ± 0.05 (0.80–1.00) (n=22)
M. i. immaculata All (n_{ai}=25)	5.45 ± 0.97 (3–8) (n=62)	2.38 ± 0.45 (1.25–3.37) (n=62)	2.30 ± 0.19 (2.06–2.72) (n=62)	3.17 ± 0.16 (2.86–3.58) (n=62)	3.10 ± 0.14 (2.86–3.43) (n=61)	0.07 ± 0.05 (-0.02-0.20) (n=61)	0.02 ± 0.06 (0.00–0.25) (n=54)	0.97 ± 0.06 (0.75–1.00) (n=52)
M. i. concepcion, Central Andes, Colombia (n_{ai}=11)	4.89 ± 0.80 (4–6) (n=27)	2.46 ± 0.39 (1.94–3.22) (n=27)	1.98 ± 0.08 (1.85–2.10) (n=27)	2.99 ± 0.15 (2.79–3.28) (n=27)	2.94 ± 0.14 (2.73–3.22) (n=27)	0.06 ± 0.05 (0.00–0.18) (n=27)	0.02 ± 0.10 (0.00–0.50) (n=26)	0.96 ± 0.06 (0.80–1.00) (n=25)
M. z. macrorhyncha Panana to Ecuador (n_{ai}=49)	9.63 ± 1.28 (7–13) (n=124)	2.74 ± 0.37 (1.99–3.76) (n=124)	3.54 ± 0.32 (2.97–4.30) (n=124)	3.48 ± 0.14 (3.08–3.79) (n=125)	3.34 ± 0.13 (3.06–3.69) (n=123)	0.14± 0.07 (0.01–0.40) (n=123)	0.03± 0.06 (0.00–0.25) (n=125)	0.96± 0.05 (0.71–1.00) (n=119)
M. z. zeledoni Panama / Costa Rica (n_{ai}=16)	9.52 ± 1.46 (7–13) (n=48)	2.27 ± 0.39 (1.50–3.34) (n=48)	4.22 ± 0.32 (3.86–5.06) (n=48)	3.63 ± 0.09 (3.39–3.81) (n=48)	3.49 ± 0.08 (3.34–3.85) (n=48)	0.14 ± 0.05 (0.01–0.22) (n=48)	0.00 ± 0.00 (0.00–0.00) (n=44)	0.97 ± 0.06 (0.83–1.00) (n=44)
M. fortis (n_{ai}=65)	9.40 ± 1.76 (4–15) (n=160)	2.67 ± 0.58 (1.10–4.38) (n=160)	3.57 ± 0.40 (2.82–4.43) (n=160)	3.01 ± 0.16 (2.64–3.52) (n=160)	3.27 ± 0.19 (2.65–3.85) (n=160)	-0.26 ± 0.13 (-0.66—0.01) (n=160)	0.64 ± 0.17 (0.33–1.00) (n=155)	0.02 ± 0.05 (0.00–0.33) (n=156)
M. melanoceps (n_{ai}=56)	5.61 ± 0.94 (3–8) (n=145)	2.24 ± 0.44 (1.03–3.38) (n=144)	2.53 ± 0.23 (2.08–3.21) (n=144)	2.40 ± 0.12 (2.13–2.68) (n=143)	2.42 ± 0.12 (1.98–2.62) (n=143)	-0.01 ± 0.07 (-0.18–0.31) (n=142)	0.48 ± 0.14 (0.20–1.00) (n=119)	0.19 ± 0.35 (0.00–1.00) (n=133)

M. goeldii (n_{ai}=75)	7.17 ± 1.30 (4–11) (*n*=175)	2.40 ± 0.40 (1.31–3.65) (*n*=174)	2.99 ± 0.22 (2.46–3.48) (*n*=174)	2.30 ± 0.08 (2.03–2.50) (*n*=179)	2.29 ± 0.08 (2.01–2.49) (*n*=173)	0.01 ± 0.04 (-0.11–0.17) (*n*=173)	0.01 ± 0.06 (0.00–0.50) (*n*=115)
							0.98 ± 0.06 (0.50–1.00) (*n*=108)

Note shape descriptions: *immaculata*: down-curved with relatively long downward tails, small initial upstroke in some recordings. *concepcion*: as *immaculata* but shorter downward tail at end. *macrorhyncha* and *zeledoni*: inverted chevron, with wider bandwidth in middle section, downstroke section stronger than upstroke in most recordings; initial upstroke small in handful of *macrorhyncha* recordings. *fortis*: starts as flattish or L-shaped notes then changes to thick downstrokes peaking at start of each note and thicker at end (where lower). *melanoceps* and *goeldii*: modulating note, of two parts, the first higher than second, but continuously delivered ('blob-downstroke'), very small upwards tail before note in some recordings.

   Change in note shape descriptions: *immaculata*: no material change in most recordings; in some recordings, first note has initial tail descending in frequency, later notes have initial tail increasing in frequency; in some recordings, first note marginally longer; otherwise no change. *concepcion*: no material change in most recordings; marginal differences in note length in some recordings. *macrorhyncha*: none in most recordings; in some, first note marginally longer, otherwise no change. *zeledoni*: first note appreciably longer. *fortis*: first notes flatter or L-shaped, later notes more like downstrokes, with gradual change. *melanoceps*: first 1–3 notes shorter and less varying in frequency than later ones; some recordings have very short note after first note, forming double note. *goeldii*: reduced differences in note lengths compared to *melanoceps*; two very short notes after first note, forming double or triple note.

B. Female songs

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of second note (kHz)	Max. frequency of last note (kHz)	Frequency variation (kHz)	Position of peak (%)	Position of trough (%)
M. i. immaculata, Mérida Andes, Venezuela (n_{ai}=5)	4.23 ± 0.44 (4–5) (*n*=13)	1.87 ± 0.21 (1.68–2.27) (*n*=13)	2.27 ± 0.06 (2.20–2.38) (*n*=13)	3.31 ± 0.25 (2.99–3.90) (*n*=13)	3.23 ± 0.21 (2.99–3.55) (*n*=13)	0.08 ± 0.10 (-0.03–0.35) (*n*=13)	0.00 ± 0.00 (0.00–0.00) (*n*=11)	1.00 ± 0.00 (1.00–1.00) (*n*=11)
M. i. concepcion, Central Andes, Colombia (n_{ai}=3)	4.42 ± 0.53 (4–5) (*n*=7)	2.06 ± 0.25 (1.83–2.54) (*n*=7)	2.15 ± 0.13 (1.97–2.31) (*n*=7)	3.36 ± 0.26 (3.10–3.73) (*n*=7)	3.23 ± 0.07 (3.18–3.35) (*n*=7)	0.13 ± 0.19 (-0.10–0.40) (*n*=7)	0.18 ± 0.24 (0.00–0.67) (*n*=7)	0.86 ± 0.31 (0.17–1.00) (*n*=7)
M. z. macrorhyncha Panama to Ecuador (n_{ai}=13)	10.35 ± 2.04 (7–18) (*n*=26)	2.43 ± 0.48 (1.81–4.40) (*n*=26)	4.27 ± 0.43 (3.61–5.02) (*n*=26)	3.78 ± 0.20 (3.55–4.39) (*n*=27)	3.52 ± 0.13 (3.33–3.73) (*n*=26)	0.24 ± 0.08 (0.13–0.41) (*n*=26)	0.01 ± 0.06 (0.00–0.28) (*n*=27)	0.97 ± 0.06 (0.82–1.00) (*n*=26)
M. z. zeledoni Panama / Costa Rica (n_{ai}=2)	9.25 ± 1.50 (7–10) (*n*=4)	1.96 ± 0.09 (1.82–2.01) (*n*=4)	4.71 ± 0.58 (3.84–5.01) (*n*=4)	3.85 ± 0.06 (3.77–3.89) (*n*=4)	3.69 ± 0.10 (3.54–3.76) (*n*=4)	0.17 ± 0.04 (0.13–0.23) (*n*=4)	0.00 ± 0.00 (0.00–0.00) (*n*=4)	1.00 ± 0.00 (1.00–1.00) (*n*=4)
M. fortis (n_{ai}=5)	7.38 ± 1.41 (5–9) (*n*=8)	2.11 ± 0.34 (1.51–2.51) (*n*=8)	3.52 ± 0.54 (3.00–4.37) (*n*=8)	3.09 ± 0.13 (2.89–3.24) (*n*=8)	3.46 ± 0.34 (3.16–3.93) (*n*=8)	-0.38 ± 0.24 (-0.69–-0.09) (*n*=8)	0.83 ± 0.12 (0.63–1.00) (*n*=8)	0.07 ± 0.10 (0.00–0.25) (*n*=8)
M. melanoceps (n_{ai}=16)	4.96 ± 0.74 (4–7) (*n*=28)	1.69 ± 0.32 (1.21–2.56) (*n*=28)	2.97 ± 0.22 (2.67–3.49) (*n*=28)	2.63 ± 0.17 (2.15–3.09) (*n*=28)	2.52 ± 0.11 (2.29–2.88) (*n*=28)	0.11 ± 0.17 (-0.33–0.58) (*n*=28)	0.31 ± 0.22 (0.00–0.67) (*n*=27)	0.67 ± 0.43 (0.00–1.00) (*n*=28)
M. goeldii (n_{ai}=12)	6.95 ± 1.33 (5–10) (*n*=22)	2.08 ± 0.39 (1.37–3.05) (*n*=22)	3.35 ± 0.25 (2.85–3.77) (*n*=22)	2.53 ± 0.16 (2.30–2.91) (*n*=22)	2.38 ± 0.09 (2.20–2.51) (*n*=22)	0.16 ± 0.13 (-0.06–0.61) (*n*=22)	0.29 ± 0.30 (0.00–1.00) (*n*=21)	0.80 ± 0.40 (0.00–1.00) (*n*=21)

Note shape descriptions: *immaculata*: down-curved. *concepcion*: down-curved in two recordings; inverted chevron, thickest in middle section with downstroke stronger in other recording. *macrorhyncha* and *zeledoni*: inverted chevron, thickest in middle section with downstroke stronger than upstroke in most recordings; upstroke stronger in one *macrorhyncha* recording. *fortis*: flattish or L-shaped notes (at start) and thick downstrokes (towards end). *melanoceps*: blob-downstrokes, up-downstrokes (inverted chevrons) and one double up-down-stroke. *goeldii*: blob-downstrokes, upwards tail before note in some recordings.

   Change in note shape desciptions: *immaculata* and *concepcion*: no material change. *macrorhyncha*: none in most recordings; first note marginally longer in some recordings; in one recording notes change from being more upstrokes to more downstrokes. *zeledoni*: first note longer. *fortis*: first notes flatter or L-shaped, later

notes more like downstrokes, with gradual change. *melanoceps*: none in some recordings; first and / or second note shorter and less varying in frequency in others; change from up-down-stroke to blob-downstroke or *vice versa* in some recordings. *goeldii*: none in some recordings; very short second or third notes (as double or triple note) after first note in most.

C. Multi-note calls

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency of highest note (kHz)	Max. frequency of lowest note (kHz)	Frequency variation (kHz)	Position of peak	Position of trough
M. i. immaculata Mérida Andes, Venezuela (n_{ai}=4)	13.56 ± 5.48 (7–24) (n=9)	0.78 ± 0.33 (0.41–1.42) (n=9)	17.58 ± 0.76 (16.88–19.14) (n=9)	6.86 ± 0.55 (6.37–7.38) (n=9)	6.02 ± 0.60 (5.46–7.02) (n=9)	0.84 ± 0.25 (0.41–1.26) (n=9)	0.20 ± 0.23 (0.00–0.56) (n=9)	0.46 ± 0.47 (0.00–1.00) (n=9)
M. z. concepcion, Central Andes, Colombia (n_{ai}=3)	12.13 ± 10.25 (3–29) (n=8)	0.80 ± 0.57 (0.23–1.73) (n=8)	13.93 ± 2.35 (10.73–16.89) (n=8)	6.72 ± 0.43 (6.27–7.34) (n=6)	6.24 ± 0.44 (5.61–6.99) (n=6)	0.43 ± 0.51 (0.02–1.40) (n=6)	0.42 ± 0.33 (0.14–1.00) (n=8)	0.56 ± 0.36 (0.00–0.95) (n=8)
M. z. macrorhyncha Panama to Ecuador (n_{ai}=26)	12.18 ± 6.17 (3–35) (n=68)	0.92 ± 0.45 (0.18–2.56) (n=68)	13.40 ± 2.37 (9.36–20.61) (n=68)	5.48 ± 0.80 (4.20–7.65) (n=68)	4.80 ± 0.69 (3.67–6.36) (n=67)	0.71 ± 0.58 (0.10– 3.58) (n=67)	0.22 ± 0.25 (0.01–1.00) (n=67)	0.60 ± 0.32 (0.00–1.00) (n=67)
M. z. zeledoni Panama / Costa Rica (n_{ai}=3)	24.71 ± 11.69 (10–40) (n=7)	1.66 ± 0.80 (0.65–2.72) (n=7)	14.89 ± 0.30 (14.51–15.41) (n=7)	5.46 ± 0.61 (4.59–5.99) (n=7)	4.62 ± 0.53 (3.88–5.20) (n=7)	0.84 ± 0.16 (0.62–1.04) (n=7)	0.42 ± 0.43 (0.04–1.00) (n=7)	0.60 ± 0.38 (0.08–1.00) (n=7)
M. fortis (n_{ai}=16)	20.21 ± 6.55 (8–37) (n=43)	1.19 ± 0.44 (0.49–2.21) (n=43)	17.48 ± 2.68 (10.61–22.94) (n=43)	5.34 ± 0.92 (4.04–7.57) (n=40)	4.55 ± 0.82 (3.08–6.22) (n=41)	0.78 ± 0.43 (0.13–1.69) (n=42)	0.18 ± 0.23 (0.00–1.00) (n=42)	0.41 ± 0.39 (0.00–1.00) (n=41)
M. melanoceps (n_{ai}=1)	15.00 ± 3.61 (11–18) (n=3)	1.39 ± 0.36 (1.00–1.72) (n=3)	10.81 ± 0.29 (10.47–10.90) (n=3)	2.77 ± 0.09 (2.66–2.83) (n=3)	2.37 ± 0.04 (2.33–2.40) (n=3)	0.39 ± 0.05 (0.33–0.43) (n=3)	0.42 ± 0.50 (0.12–0.99) (n=3)	0.58 ± 0.14 (0.45–0.73) (n=3)
M. goeldii (n_{ai}=12)	14.26 ± 5.86 (3–24) (n=31)	1.36 ± 0.56 (0.29–2.76) (n=31)	10.56 ± 1.82 (8.69–18.15) (n=42)	2.70 ± 0.21 (2.38–3.42) (n=31)	2.34 ± 0.23 (2.00–2.92) (n=31)	0.36 ± 0.17 (0.05–0.73) (n=31)	0.11 ± 0.19 (0.01–0.73) (n=31)	0.59 ± 0.39 (0.00–1.00) (n=31)

Note shape descriptions: *immaculata, concepcion, macrorhyncha, zeledoni, fortis*: upstrokes, with small downstroke or blob at end. *melanoceps*: up-down-stroke, with downstroke stronger and very small upstroke. *goeldii*: up-down stroke, with downstroke stronger on most recordings; upstroke part is small on some recordings.

D. Single-note calls

Taxon	No. of notes	Call duration (s)	Max. frequency of highest note (kHz)
M. i. immaculata Mérida Andes, Venezuela (n_{ai}=2)	1 (all) (n=6)	0.07 ± 0.02 (0.05–0.11) (n=6)	4.13 ± 0.14 (3.93–4.30) (n=6)
M. i. immaculata East Andes, Colombia (n_{ai}=2)	1 (all) (n=6)	0.13 ± 0.12 (0.11–0.16) (n=6)	4.43 ± 0.21 (4.20–4.67) (n=6)
M. i. immaculata All (n_{ai}=4)	1 (all) (n=12)	0.10 ± 0.04 (0.05–0.16) (n=12)	4.28 ± 0.23 (3.93–4.67) (n=12)
M. z. concepcion, Central Andes, Colombia up-down (n_{ai}=2)	1 (all) (n=6)	0.13 ± 0.02 (0.09–0.15) (n=6)	3.99 ± 0.06 (3.91–4.05) (n=6)
M. z. concepcion downstroke (n_{ai}=6)	1 (all) (n=15)	0.15 ± 0.04 (0.09–0.20) (n=15)	3.91 ± 0.34 (3.49–4.42) (n=15)
M. z. macrorhyncha Panama to Ecuador (n_{ai}=20)	1 (all) (n=15)	0.15 ± 0.04 (0.10–0.20) (n=15)	3.91 ± 0.34 (3.49–4.42) (n=15)

M. i. zeledoni Panama / Costa Rica (n_{ai}=2)	1 (all) (n=6)	0.09 ± 0.02 (0.06–0.11) (n=6)	4.24 ± 0.24 (4.13–4.79) (n=6)
M. fortis (n_{ai}=4)	1 (all) (n=9)	0.05 ± 0.03 (0.02–0.08) (n=9)	3.72 ± 0.22 (3.30–4.02) (n=9)
M. melanoceps (n_{ai}=11)	1 (all) (n=26)	0.11 ± 0.01 (0.06–0.12) (n=25)	2.56 ± 0.17 (2.34–3.09) (n=26)
M. goeldii (n_{ai}=7)	1 (all) (n=21)	0.12 ± 0.01 (0.09–0.14) (n=21)	2.40 ± 0.13 (2.13–2.56) (n=21)

Note shape descriptions: *immaculata, concepcion* (up-down) and *fortis*: up-down stroke. *concepcion* downslurred call: downstroke, small blob at start or thin upstroke at start. *macrorhyncha* and *zeledoni*: up-down stroke, thicker and longer at peak in most recordings. *melanoceps* and *goeldii*: up-down stroke, thicker and longer at peak, and skewed higher frequency at start; shape broken in one recording of *goeldii*.

Appendix 4: differences between *Myrmeciza* taxa

Differences between *M. immaculata* populations are shown using diagnosability levels described under Methods.

The following codes are used:
For vocal variables, the first symbol refers to the type of call:
♂: male song
♀: female song
σ: single-note call
Σ: single-note downslurred call of *concepcion*
μ: multi-note call

The following codes refer to vocal variables:
NN: number of notes
SL: song length
SS: song speed
MF: for songs: acoustic frequency of second note; for calls: max. acoustic frequency.
mF: for songs: acoustic frequency of last note; for calls: min. acoustic frequency
FV: acoustic frequency variation
CP: change of pace
PP: position of peak in acoustic frequency
PT: position of trough in acoustic frequency
NS: note shape
CNS: change in note shape

For biometrics, the following codes are used:
WI: wing length
TL: tail length
TR: tarsus length
BL: bill length
BW: bill width
MS: mass.

N/A: no sample available for one of the populations for the type of vocalisation in question
No diff: no observed differences in any variables measured as determined by statistical tests

Degrees of freedom can be calculated by taking the lower value of the two taxa for the relevant variable under '(n=x)' in Appendices 2–3, and subtracting 1. The taxon with the higher or lower of the relevant variable can be seen in Appendices 1–2. Differences in bold denote that the two taxa are phylogenetic species *sensu* Cracraft 1983) based on the relevant variable. The two layers of shading represent new species limits proposed herein. See the sample sizes in previous appendices when undertaking pairwise comparisons. Note that some populations may appear 'less diagnosable' for certain variables than they may actually be due to sample size: all statistical tests are affected by sample size. For example, there are particularly small samples of biometrics for *goeldii*, of female songs for several populations especially *zeledoni*, and of multi-note calls for *melanoceps*

	M. i. immaculata	M. i. concepcion	M. z. macrorhyncha	M. z. zeledoni	M. fortis	M. melanoceps	M. goeldii
M. i. immaculata Mérida Andes							
Songs (♂)	X	♂SS(1,2); ♂NS(4)	♂NN(1,2,3); ♂SL(1); ♂SS(1,2,3,4,5); ♂MF(1,2); ♂mF(1); ♂FV(1); ♂NS(4)	♂NN(1,2); ♂SS(1,2,3,4,5); ♂MF(1,2,3); ♂mF(1,2,3,4,5); ♂FV(1); ♂NS(4)	♂NN(1,2); ♂SS(1,2,3,4,5); ♂MF(1); ♂mF(1); ♂FV(1,2); ♂PP(1,2,3,4,5); ♂PT(1,2,3,4,5); ♂NS(4); ♂CNS(4)	♂SS(1); ♂MF(1,2,3,4,5); ♂mF(1,2,3,4,5); ♂FV(1); ♂PP(1,2,3,4,5); ♂PT(1,2); ♂NS(4); ♂CNS(4)	♂NN(1); ♂SS(1,2,3,5); ♂MF(1,2,3,4,5); ♂mF(1,2,3,4,5); ♂FV(1); ♂NS(4); ♂CNS(4)
Songs (♀)	X	♀: No diff.	♀NN(1,2,3,4,5); ♀SL(1); ♀SS(1,2,3,4,5); ♀MF(1); ♀mF(1); ♀FV(1); ♀NS(4)	♀NN(2,4); ♀SS(2,4,5); ♀MF(1,2); ♀mF(1,2); ♀NS(4); ♀CNS(4)	♀NN(1,2); ♀SS(2,4); ♀FV(2,4); ♀PP(1,2,3,4,5); ♀PT(1,2,3,4,5); ♀NS(4); ♀CNS(4)	♀SS(1,2,4,5); ♀MF(1,2); ♀mF(1,2); ♀PP(1,2); ♀NS(4); ♀CS(4)	♀NN(1,2); ♀SS(1,2,3,4,5); ♀MF(1,2,4); ♀mF(1,2,3,4,5); ♀PP(1); ♀NS(4); ♀CNS(4)
Calls	X	♂SL(1); ♂MF(1)	♂SL(1); ♂NS(4)	♂MF(1); ♂NS(4)	♂MF(1)	♂SL(1); ♂MF(1,2,3,4,5); ♂NS(4)	♂SL(1,2); ♂MF(1,2,3,4,5); ♂NS(4)
		μ: No diff.; ΣSL(1,2); ΣNS(4)	μSS(1,2); μMF(1); μmF(1)	μSS(1,2,3,4,5); μMF(2,4); μmF(1,2,4)	μMF(1); μmF(1)	μSS(2,3,4,5); μMF(1,2,3,4,5); μmF(1,2,3,4,5); μFV(2); μNS(4)	μSL(1); μSS(1,2,3,5); μMF(1,2,3,4,5); μmF(1,2,3,4,5); μFV(2); μNS(4)
M. i. immaculata East Andes	X						
Plumage 'X' Songs (♂)	X	♂SS(1,2); ♂mF(1); ♂NS(4)	♂NN(1,2,3); ♂SS(1,2,3,4,5); ♂MF(1); ♂mF(1); ♂NS(4)	♂NN(1,2); ♂SS(1,2,3,4,5); ♂MF(1,2); ♂mF(1,2); ♂NS(4)	♂NN(1,2); ♂SS(1,2,3,4); ♂MF(1); ♂FV(1,2,3,4,5); ♂PP(1,2,3,4,5); ♂PT(1,2,3,4,5); ♂NS(4); ♂CNS(4)	♂MF(1,2,3,4,5); ♂mF(1,2,3,4,5); ♂FV(1); ♂PP(1,2,3); ♂PT(1,2); ♂CNS(4)	♂NN(1); ♂SS(1,2); ♂MF(1,2,3,4,5); ♂mF(1,2,3,4,5); ♂FV(1,2); ♂NS(4); ♂CNS(4)

	M. i. immaculata	M. i. concepcion	M. z. macrorhyncha	M. z. zeledoni	M. fortis	M. melanoceps	M. goeldii
Plumage 'X' Songs (♀)	X	♀: N/A	♀: N/A	♀: N/A	♀: N/A	♀: N/A	♀: N/A
Biometrics 'X' Calls	X	σMF(1,2,4)	σSL(1) σMF(1) σNS(4)	σSL(1,2) σNS(4)	σSL(1,2,4) σMF(1,2,4)	σSL(1) σMF(1,2,3,4,5) σNS(4)	σMF(1,2,3,4,5) σNS(4)
	μ: N/A	μ: N/A ΣMF(1) ΣNS(4)	μ: N/A	μ: N/A	μ: N/A	μ: N/A	μ: N/A
M. i. immaculata All							
Plumage 'X' Songs (♂)	X	σSS(1,2) σMF(1) σmF(1) σNS(4)	σNN(1,2,3) σSL(1) σSS(1,2,3,4,5) σMF(1,2) σmF(1) σNS(4)	σNN(1,2) σSS(1,2,3,4,5) σMF(1,2,3) σmF(1,2) σNS(4)	σNN(1,2) σSL(1) σSS(1,2,3,4,5) σMF(1) σFV(1,2) σPP(1,2,3,4,5) σPT(1,2,3,4,5) σNS(4) σCNS(4)	σSS(1) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1) σPP(1,2,3,5) σPT(1,2) σNS(4) σCNS(4)	σNN(1) σSS(1,2,3) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1) σNS(4) σCNS(4)
Plumage 'X' Songs (♀)	X	♀: No diff.	♀NN(1,2,3,4,5) ♀SL(1) ♀SS(1,2,3,4,5) ♀MF(1) ♀mF(1) ♀FV(1) ♀NS(4)	♀NN(2,4) ♀SS(2,4,5) ♀MF(1,2) ♀mF(1,2) ♀NS(4)	♀NN(1,2) ♀SS(2,4) ♀FV(2,4) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀SS(1,2,4,5) ♀MF(1,2) ♀mF(1,2) ♀PP(1,2) ♀NS(4) ♀CS(4)	♀NN(1,2) ♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)
Biometrics 'X' Calls	X	σMF(1) μ: No diff. ΣSL(1) ΣNS(4)	σMF(1) σNS(4) μSS(1,2) μMF(1) μmF(1)	σNS(4) μSS(1,2,3,4,5) μMF(2,4) μmF(1,2,4)	σMF(1,2) μMF(1) μmF(1)	σMF(1,2,3,4,5) σNS(4) μSS(2,3,4,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(2) μNS(4)	σMF(1,2,3,4,5) σNS(4) μSL(1) μSS(1,2,3,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(2) μNS(4)

	M. i. immaculata	M. i. concepcion	M. z. macrorhyncha	M. z. zeledoni	M. fortis	M. melanoceps	M. goeldii
M. i. concepcion							
Plumage |X| Songs (♂)	Male *concepcion* has less extensive feathering on forehead.	X	♂NN(1,2,3,4,5) ♂SS(1,2,3,4,5) ♂MF(1,2) ♂mF(1,2) ♂FV(1) ♂NS(4)	♂NN(1,2,3,4,5) ♂SS(1,2,3,4,5) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1) ♂NS(4) ♂CNS(4)	♂NN(1,2) ♂SS(1,2,3,4,5) ♂mF(1,2) ♂FV(1,2,4) ♂PP(1,2,3,5) ♂PT(1,2,3,4,5) ♂NS(4) ♂CNS(4)	♂NN(1) ♂SS(1,2) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4) ♂FV(1) ♂PP(1,2,3) ♂PT(1,2) ♂NS(4)	♂NN(1,2) ♂SS(1,2,3,4,5) ♂MF(1,2,3,4,5) ♂mF(1,2,3,4,5) ♂FV(1) ♂NS(4) ♂CNS(4)
Plumage |X| Songs (♀)	Female *concepcion* has average greyer wash on breast and averages less rufous on undertail-coverts and flanks.	X	♀NN(1,2,3,4,5) ♀SS(1,2,3,4,5) ♀mF(1,2)	♀NN(2,4) ♀SS(2,4,5) ♀MF(2,4) ♀mF(1,2,4) ♀CNS(4)	♀NN(2) ♀SS(2) ♀PP(1,2) ♀PT(2) ♀NS(4) ♀CNS(4)	♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5)	♀NN(1,2) ♀SS(1,2,3,4,5) ♀MF(1,2,4) ♀mF(1,2,3,4,5) ♀NS(4)
Biometrics |X| Calls	No diff.	X	σNS(4) ΣSL(1) ΣNS(4) μmF(1,2)	σSL(1) σMF(1,2,4) σNS(4) ΣSL(1,2) ΣMF(1) ΣNS(4) μMF(4) μmF(1,2,4)	σSL(1,2,4) σMF(1) ΣSL(1,2,4) ΣNS(4) μMF(1) μmF(1,2)	σMF(1,2,3,4,5) σNS(4) ΣSL(1) ΣMF(1,2,3,4,5) ΣNS(4) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μNS(4)	σMF(1,2,3,4,5) σNS(4) ΣSL(1) ΣMF(1,2,3,4,5) ΣNS(4) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μNS(4)
M. z. macrorhyncha							
Plumage |X| Songs (♂)	Male: *macrorhyncha* has more extensive white patch on shoulder and less extensive feathering on forehead.	Male: *macrorhyncha* has more extensive white patch on shoulder.	X	σSL(1) σSS(1,2) σMF(1) σmF(1) σPP(1) σCNS(4)	σMF(1,2,3) σFV(1,2,3,4,5) σPP(1,2,3,4,5) σPT(1,2,3,4,5) σNS(4) σCNS(4)	σNN(1,2,3) σSL(1) σSS(1,2,3) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1,2) σPP(1,2,3,4,5) σPT(1,2) σNS(4) σCNS(4)	σNN(1) σSL(1) σSS(1,2) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1,2) σNS(4) σCNS(4)

	M. i. immaculata	M. i. concepcion	M. z. macrorhyncha	M. z. zeledoni	M. fortis	M. melanoceps	M. goeldii
Plumage │X│ Songs (♀)	Female *macrorhyncha* has more extensive white patch on shoulder, less contrasting crown, and more uniform and intensely rufous underparts and upperparts.		X	♀SL(1) ♀CNS(4)	♀NN(1) ♀MF(1,2,3,4) ♀FV(1,2,4) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀NN(1,2) ♀SL(1) ♀SS(1,2) ♀MF(1,2,3,5) ♀mF(1,2,3,5) ♀PP(1)	♀NN(1,2) ♀SS(1,2) ♀SL(1) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀NS(4)
Biometrics │X│ Calls	BL(1,2) TL(1) TR(1)	TL(1) TR(1) BL(1)	X	σMF(1) μ: No diff.	σSL(1,2) σMF(1) σNS(4) μNN(1) μSL(1) μSS(1)	σMF(1,2,3,4,5) σNS(4) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1) μNS(4)	σSL(1) σMF(1,2,3,4,5) σNS(4) μSS(1) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1) μNS(4)
M. z. zeledoni							
Plumage │X│ Songs (♂)			Male: *zeledoni* has more extensive white patch on shoulder.	Male: *zeledoni* has less extensive white patch on shoulder. X	σSS(1) σMF(1,2,3,5) σmF(1) σFV(1,2,3,4,5) σPP(1,2,3,4,5) σPT(1,2,3,4,5) σNS(4) σCNS(4)	σNN(1,2) σSS(1,2,3,4,5) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1,2) σPP(1,2,3,4,5) σPT(1,2) σNS(4) σCNS(4)	σNN(1) σSL(1) σSS(1,2,3,4,5) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1,2) σNS(4) σCNS(4)
Plumage │X│ Songs (♀)	Female: *macrorhyncha* has more extensive white patch on shoulder, less contrasting crown, and more uniform and intensely rufous underparts and upperparts.		Female: *zeledoni* has less extensive white patch on shoulder.	X	♀MF(1,2,3,4,5) ♀FV(1,2,4) ♀PP(1,2,3,4,5) ♀PT(1,2,3,4,5) ♀NS(4) ♀CNS(4)	♀NN(4) ♀SS(2) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀PP(1,2) ♀CNS(4)	♀SS(2,4) ♀MF(1,2,3,4,5) ♀mF(1,2,3,4,5) ♀PP(1) ♀NS(4) ♀CNS(4)

	M. i. immaculata	M. i. concepcion	M. z. macrorhyncha	M. z. zeledoni	M. fortis	M. melanoceps	M. goeldii
Biometrics !X! Calls	BL(1)	No diff.	WL(1) TR(1) BL(1)	X	σSL(1) σMF(1,2,4) σNS(4) μSS(1) μNS(4)	σMF(1,2,3,4,5) σNS(4) μSS(2,3,4,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1,2,4) μNS(4)	σSL(1) σMF(1,2,3,4,5) σNS(4) μSS(1,2) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1,2) μNS(4)
M. fortis **Plumage !X! Songs (♂)**	M. fortis has greyer mantle and blue (not whitish) bare skin behind eye.	M. fortis has greyer mantle and blue behind eye.	M. fortis has greyer mantle and blue (not whitish) bare skin behind eye, and less extensive white feathering on shoulder.	M. fortis has greyer mantle and blue (not whitish) bare skin behind eye.	X	σNN(1,2) σSL(1) σSS(1,2) σMF(1,2,3,5) σmF(1,2,3,4,5) σFV(1,2) σPP(1) σPT(1) σNS(4) σCNS(4)	σNN(1) σSL(1) σSS(1) σMF(1,2,3,4,5) σmF(1,2,3,4,5) σFV(1,2) σPP(1,2,3,5) σPT(1,2,3,4,5) σNS(4) σCNS(4)
Plumage !X! Songs (♀)	M. fortis has brighter rufous on crown, paler brown mantle, grey (not brown) on breast and blue (not whitish) bare skin behind eye.				X	♀MF(1) ♀mF(1,2) ♀FV(1,2) ♀PP(1,2) ♀PT(1,2) ♀NS(4) ♀CNS(4)	♀MF(1,2,3) ♀mF(1,2,4,5) ♀FV(1,2,4) ♀PP(1,2) ♀PT(1,2) ♀NS(4) ♀CNS(4)
Biometrics !X! Calls	TL(1,2) TR(1) BL(1)	TL(1,2) TR(1)	TL(1) TR(1) BL(1)	WL(1) TL(1,2)	X	σSL(1,2) σMF(1,2,3,4,5) σNS(4) μSS(2,5) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μFV(1) μNS(4)	σSL(1,2,4) σMF(1,2,3,4,5) σNS(4) μNN(1) μSS(1,2) μMF(1,2,3,4,5) μmF(1,2,3,4,5) μNS(4)

	M. i. immaculata	M. i. concepcion	M. z. macrorhyncha	M. z. zeledoni	M. fortis	M. melanoceps	M. goeldii
M.melanoceps							
Plumage |X| Songs (♂)	M. melanoceps has white interscapular patch, more extensive white feathering on shoulder and darker, less extensive bare skin in ocular region.		M. melanoceps has white interscapular patch, and darker, less extensive bare skin in ocular region.	M. melanoceps has white interscapular patch and darker bare skin.	M. melanoceps has white interscapular patch.	X	♂NN(1) ♂SS(1,2) ♂MF(1) ♂mF(1) ♂FV(1) **♂PP(1,2,3,5)** ♂PT(1,2) **♂CNS(4)**
Plumage |X| Songs (♀)	M. melanoceps is more orange throughout, has black hood and darker, less extensive bare skin in ocular region.		M. melanoceps is more orange throughout, has black hood and darker, less extensive bare skin in ocular region.		M. melanoceps is more orange throughout and has a black hood, whilst fortis is dingier brown on upperparts, has grey on underparts and brighter blue bare skin in ocular region.	X	♀SS(1) ♀mF(1)
Biometrics |X| Calls	WL(1) **TL(1,2,3,4,5)** BL(1,2)	WL(1,2) **TL(1,2,3,4,5)** BL(1,2)	WL(1) **TL(1,2,3,4,5)** TR(1) BL(1)	WL(1,2) **TL(1,2,3,4,5)** TR(1,2) BL(1)	WL(1) TL(1) TR(1) BL(1)	X	♂SL(1) ♂MF(1)
							μ: No diff.
M. goeldii							
Plumage (♂)	M. goeldii has brighter red (not reddish-brown) iris, lacks extensive bare skin in ocular region, lacks darker wing bend and has white interscapular patch.		M. goeldii has brighter red (not reddish-brown) iris, lacks extensive bare skin in ocular region, lacks darker throat, lacks extensive bare skin in ocular region, lacks white on wing bend and has white interscapular patch.			M. melanoceps has brown (not red) iris and more extensive bare skin in ocular region.	X
Plumage (♀)	M. goeldii is more orange-brown generally, has whitish (not dark) throat, lacks darker tail and has less extensive bare skin in ocular region.		M. goeldii is more orange-brown generally, has brighter rufous crown, darker brown mantle and is grey (not orange) on breast.		M. fortis has brighter rufous crown, darker brown mantle and is grey (not orange) on breast.	M. melanoceps has brown (not red) iris and black hood, whilst goeldii has dusky face and whitish throat. M. melanoceps has more extensive bare skin in ocular region.	X
Biometrics	No diff.	No diff.	No diff.	No diff.	No diff.	No diff.	X

Note: differences between East Andes and Mérida Andes populations of M. immaculata in voice: ♂MF(1). ♀: N/A. ♂SL(1,2,4), ♂MF(1), μ: N/A